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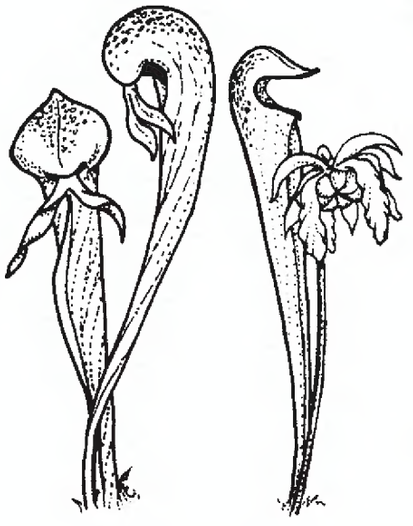

CARNIVOROUS PLANT NEWSLETTER

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Front Cover: *Exyra semicrocea* larva in *Sarracenia flava* pitcher, Liberty Co., Florida. Photo by Barry Rice. Article on page 75.

Back Cover: Typical *Exyra* larva-eaten *Sarracenia flava* pitcher. Photo by Djoni Crawford. Article on page 75.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

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Erratum: The DOI listed for New cultivars on page 55 of the March 2024 issue of CPN is a duplicate. It is corrected to be https://doi.org/10.55360/cpn531.cv531 online and in the PDF versions.

Expanding our scope: a larger endangered species restoration project for *Sarracenia oreophila* in Alabama

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In March 2024, a crew of nearly forty volunteer conservation workers will converge in northeastern Alabama to spend long days cutting and clearing brush, coordinating habitat burns, and taking valuable data to preserve critical sites containing native *Sarracenia oreophila* plants.

The team leadership, centered at the Arboretum at Auburn University, recruits and trains the volunteer project crew. Ultimately, they seek to meet the goals of the federal *Sarracenia oreophila* recovery plan, once thought to be practically unobtainable. But in a rare win for conservation, diligent hard work in habitat restoration has breathed new life into that dream.

These important sites of *Sarracenia oreophila* are maintained and carefully monitored. To be able to do this work on private land, the team has painstakingly gained the trust and confidence of the collected landowners.

The project leaders were surprised that their project had been noticed by the ICPS and have been grateful for our financial support. To adequately address the long list of objectives, the team needs help and time. The ICPS increased its financial support this year to allow this group to better achieve their goals. This restoration work is turning out to be an unequivocal success, but needs continuing work long into the future. Please help us continue our support by donating to the ICPS conservation fund.

Commemorating the life and career of Katsuhiko Kondo with the 2024 ICPS Lifetime Achievement Award

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We are pleased to commemorate the life and work of Katsuhiko Kondo (Ja.: 近藤勝彦; b. 1944), professor of botany at Hiroshima University in Japan, as the recipient of the 2024 ICPS Lifetime Achievement Award. The ICPS Lifetime Achievement Award is presented in recognition of an individual's outstanding leadership and contribution to the world of carnivorous plants through research, cultivation, conservation, or in other ways deemed to be above and beyond the everyday with a significant impact on the field. Kondo has been monumental and formative in each of these ways at a global level, and his work has influenced research, cultivation, and popular knowledge. Kondo has helped to connect the global carnivorous plant community of scholars and enthusiasts alike since before this journal's inception in 1972.

Figure 1: Katsuhiko Kondo – photographer unknown, reproduced from Allen Lowrie's Magnum Opus.

Kondo has spent his entire life engrossed in the study of carnivorous plants. He made important scientific findings early-on studying the karyotypes of various carnivorous plant genera. From the 1980s into the early 2000s Kondo would continue to research the phylogenetics and systematic morphology of *Drosera*, *Pinguicula*, *Utricularia*, and *Aldrovanda*, a legacy of study continued by his students. Kondo pursued many other original research projects on carnivorous plants. He introduced to science and published several noteworthy new species, including taxa in the *Drosera petiolaris* complex and in *Nepenthes*.

In Japan, Kondo is also revered for his formative role in popularizing the carnivorous plant interest there by means of the books he authored with his father, Masahiro, in 1972 and 1983. These were nearly the first books in the world to address all known carnivorous plant genera for a general audience. They are popular outside Japan and are highly sought by enthusiasts even today.

Kondo would publish 12 technical papers in the CPN. His first article, Kondo 1972, was a brief English-language history of the Insectivorous Plant Society of Japan (IPSJ), the first modern organization devoted to carnivorous plants. Most of Kondo's CPN publications later would concern the phylogeny, physiology, and tissue-culture of *Drosera*, *Dionaea*, *Utricularia*, and *Aldrovanda*. This work has been continued and expanded upon by his students, including Yoshikazu Hoshi and Mitsuyasu Hasebe. They continue to pursue the same areas of study Kondo did in the 1970s.

Some of Kondo's career highlights include the following research and publications:

- His discovery of diffused-centromeric chromosomes in *Drosera*, which he researched while at Hiroshima University.

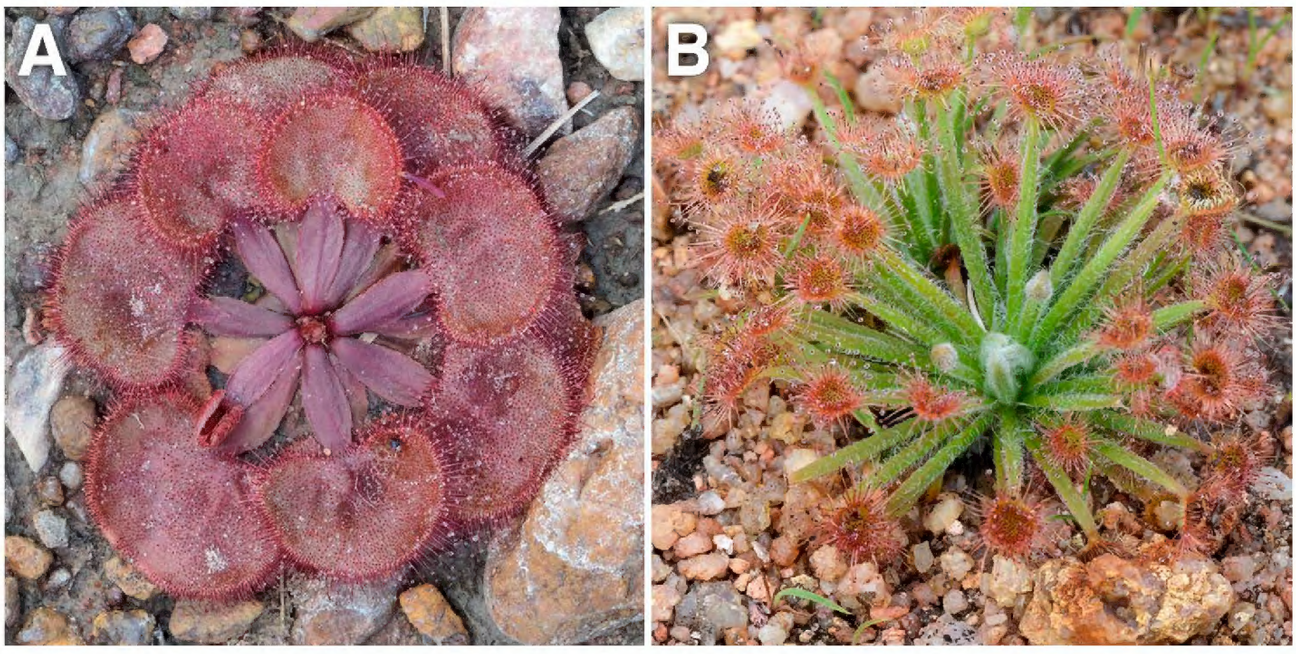

Figure 2: (A) *Drosera falconeri* K.Kondo 1984 near Darwin, NT, Australia. (B) *Drosera lanata* K.Kondo 1984 at Undarra, QLD, Australia. Photos by Richard Nunn.

- The interior of *Utricularia* seeds consists of an undifferentiated embryo, freely differentiating organs in response to their aquatic environment.
- As carnivorous plants prefer closed ecosystems with nutrient-poor soil, by purely adjusting nitrogen components their life history can be fully controlled.
- Kondo described the chromosome count for *Triphyophyllum* for the first time in 1973 (Phyton 31: 1-2) and continued to study *Utricularia*.

Kondo's short CV reads as follows:

Professor, Graduate School of Science. PhD. Born 1944. Graduated from the Tokyo University of Agriculture in 1968, and in 1975 completed a doctoral program in Botany at the University of North Carolina at Chapel Hill in the United States, attaining a PhD.

In March 1976, accepted a position as lecturer in the Biology Department at the University of Maryland, College Park, USA; in October of the same year, became a research associate in the Faculty of Integrated Arts and Science at Hiroshima University. In November of 1979, became a lecturer in the same faculty, and in April of 1980, was made an advisor for the Graduate School of Environmental Studies, also at Hiroshima University. Appointed associate professor within the same school in April of 1982, and, in April of 1988, appointed advisor for the Graduate School of Biosphere Science at Hiroshima University. In April of 1989, attained the role of professor within the Faculty of Science at Hiroshima, as well as those of advisor for the Graduate School of Science and director of the Laboratory of Plant Chromosome and Gene Stock within that faculty.

In 1993, served as a faculty advisor for the Department of Gene Science in the Graduate School of Science at Hiroshima University; and in 2000, served as advisor for the Department of Biological Science in the Graduate School of Science, also attaining the role of director at the Laboratory of Plant Chromosome and Gene Stock within the same school.

Developed a cryopreservation protocol for wild orchidaceous plants integrating abscisic acid and a desiccation process and modified it into a generalized technique, winning an

academic award from the Nagoya International Orchid Congress in 1997 and an honorable mention from the 7th Asia Pacific Orchid Conference in 2001.

In his own Hiroshima University autobiography, Kondo provides an account of his lifetime fascination with plants and in particular, carnivorous plants. It is an account that should be shared and that will no doubt resonate with those reading this award announcement.

> Counting back to the time I put out my first paper, my research career has already spanned 35 years. Looking back on my experiences within that time, I am struck by the belief that all across the world, all those who pursue botany possess a certain universal character: "Many people enjoy playing golf, baseball, soccer and so on with their friends as time carries them along, but these plant-loving people spend that time being fascinated with plants. Since they're plant-lovers, plants are all they think about."
>
> There are two things which have made me so devoted to plants—or perhaps I should say, two encounters with plants that enthralled me so. The first was when I was a second-grader on summer break, and my father let me come along with him to collect plants on Mount Ibuki, which lies on the border of Gifu and Shiga prefectures. The fields of flowers we walked through at its peak were so incredibly striking and beautiful, I can still picture them to this day.
>
> The second was when I was a fourth-grader; my father ordered from Yokohama some carnivorous plants called Venus flytraps, still a rarity among rarities at the time, and we began cultivating them. The flytrap is a plant with pairs of leaves like the halves of a clam shell that quickly spring shut to trap insects—practically every day, I'd have visitors coming over to observe these bizarrely un-plant-like moving plants. Of these, a couple became regular guests, and they even started bringing their parents along, who pestered my father to sell them some specimens—He found this quite annoying, but personally I was totally thrilled to have something people couldn't find anywhere else. For me, these two experiences were so remarkable that there was never any chance of me forgetting about them, or of even considering a different field.
>
> By the time I was in sixth grade, I was already convinced that the only life for me was one of working with plants. I also chose to study botany in graduate school, choosing a location which included natural habitats for Venus flytraps. Though my specific area of research in graduate school was different, I was always going off to see these flytrap habitats. Working with my beloved plants, my studies never seemed all that demanding. I cannot say that as the years have gone by, my feelings toward plants have remained unchanged; rather, I've become more and more devoted to them as a topic of study.

The ICPS and carnivorous plant community congratulates Katsuhiko Kondo on his lifetime's work, which this award recognizes and commemorates. Botanical artist Francois Mey, commissioned by the ICPS to mark this occasion, has painted *Drosera falconeri*, an iconic species described by Kondo in 1984.

Acknowledgements: We wish to thank Kenji Fukushima and Leo Song for their valuable knowledge and insight into Kondo's career and accomplishments; Koji Kondo (no relation to Katsuhiko Kondo) for his tireless help and direction; François Mey for his excellent commemorative painting; and Chris Springfield for expertly translating academic Japanese into English.

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Figure 3: Painting of *Drosera falconeri* K.Kondo 1984, watercolour on paper, Francois Mey.

Pinguicula lusitanica and *P. crystallina* subsp. *hirtiflora* traps

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Butterworts from the relatives around *Pinguicula vulgaris* (creating hibernacula) have a well-known characteristic – the ability to roll edges of their leaves after catching larger prey. The fact that they react in a slightly different way than the leaves of sundews was already described in CPN years ago (Studnička 2001).

Motile leaves are not reported in any of the American tropical homophyllous species. As far as I can see, the leaf margins do not roll in *P. albida*, *P. jackii* (Cuba), *P. ionantha*, *P. primuliflora*, or *P. planifolia* (USA). Transforming leaf shape into a roll is a modern adaptation. It is therefore not logical to assume a margin roll in *P. lusitanica* L., which has archaic characters: It is tropically homophyllous, has isolobate corollas, and its seedlings have two cotyledons (compared to the single cotyledon of the mentioned modern butterworts).

However, Darwin (1875) recognized that the pale butterwort was a particularly interesting European species and experimented with it as well (Darwin 1875: 392). He described his attempt as follows:

> "A moderately sized and angular bit of albumen was placed on one side of a leaf, halfway between the midrib and the naturally involuted margin. In 2 hrs. 15 m. the glands poured forth much secretion, and this side became more infolded than the opposite one. The inflection increased, and in 3 hrs. 30 m. extended up almost to the apex. After 24 hrs. the margin was rolled into a cylinder, the outer surface of which touched the blade of the leaf and reached to within the 1/20 of an inch of the midrib. After 48 hrs. it began to unfold, and in 72 hrs. was completely unfolded. The cube was rounded and greatly reduced in size; the remainder being in a semi-liquefied state."

As written by Terentius BC, "*duo cum faciunt idem, saepe non est idem*" (when two do the same thing, it is often not the same thing), and so I imitated Darwin's previous experiment just to be sure.

Methods

I placed a frozen (and then thawed) daphnia on *P. lusitanica* leaves and watched the movement response. I placed a live housefly on a leaf of the more robust *P. crystallina* subsp. *hirtiflora* (Ten.) Strid and again watched the movement response. Both plants were cultivated. The first experiment was inspired by Darwin's research (Darwin 1875). The second attempt is, I believe, new for this experimental object.

Results

On a leaf of *P. lusitanica*, I placed the frozen macerated daphnia so that the digestible substances work immediately. It took less than a day for the leaf to form into a "carnivorous roll". Compared to *P. grandiflora* or *P. vulgaris*, there was a noticeable difference here: The roll does not arise from one or the other edge of the leaf, but the entire leaf is transformed into a roll by bringing the edges together. After 4.5 days, digestion had apparently ended, as the younger, more active leaf had already begun to return to its original shape (Fig. 1).

But how is it with *P. crystallina* subsp. *hirtiflora*, the other homophyllous species native to Europe? I have not been able to find in the literature any report on whether it also has movable leaves that roll their edges. So, I subjected it to the same experiment.

Due to the larger size of the leaf, I used a live fly as food. Within an hour it was clear that the leaf worked the same way as *P. lusitanica*. The situation 6 hours after the placement of food was interesting in that the live fly got out of its original place by its own doing. In 24 hours from the start of the experiment, the leaf began to open, and after another 5 hours it was already quite obvious. The leaf returned to its original shape finally (Fig. 2).

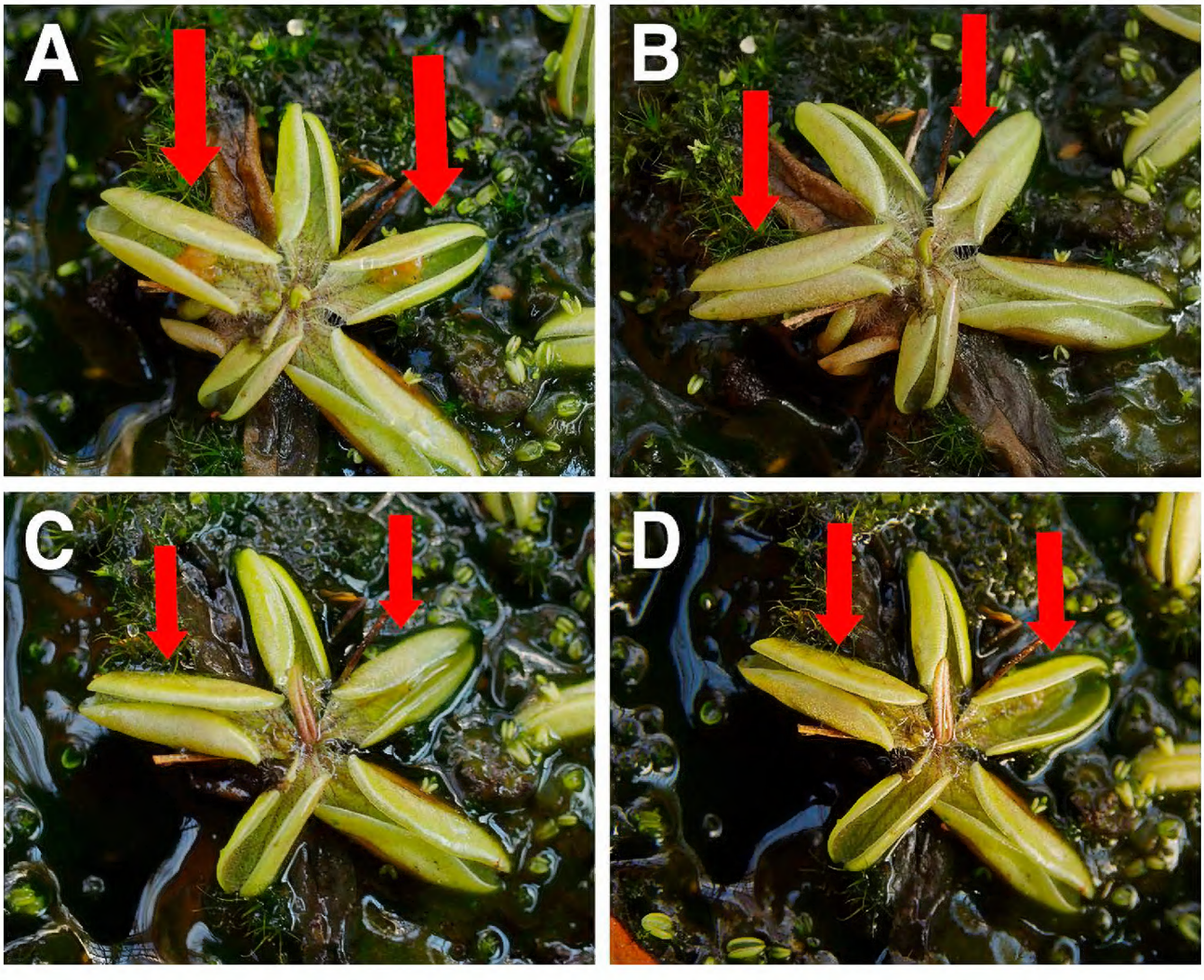

Figure 1: *Pinguicula lusitanica*: (A) Time 0, food was placed. (B) Time 19 hours, by joining the edges of the leaf, a carnivorous roll was created. (C) Time 113 hours, end of digestion, the edges of the leaves started to move away. (D) Time 128 hours, the right leaf has already opened.

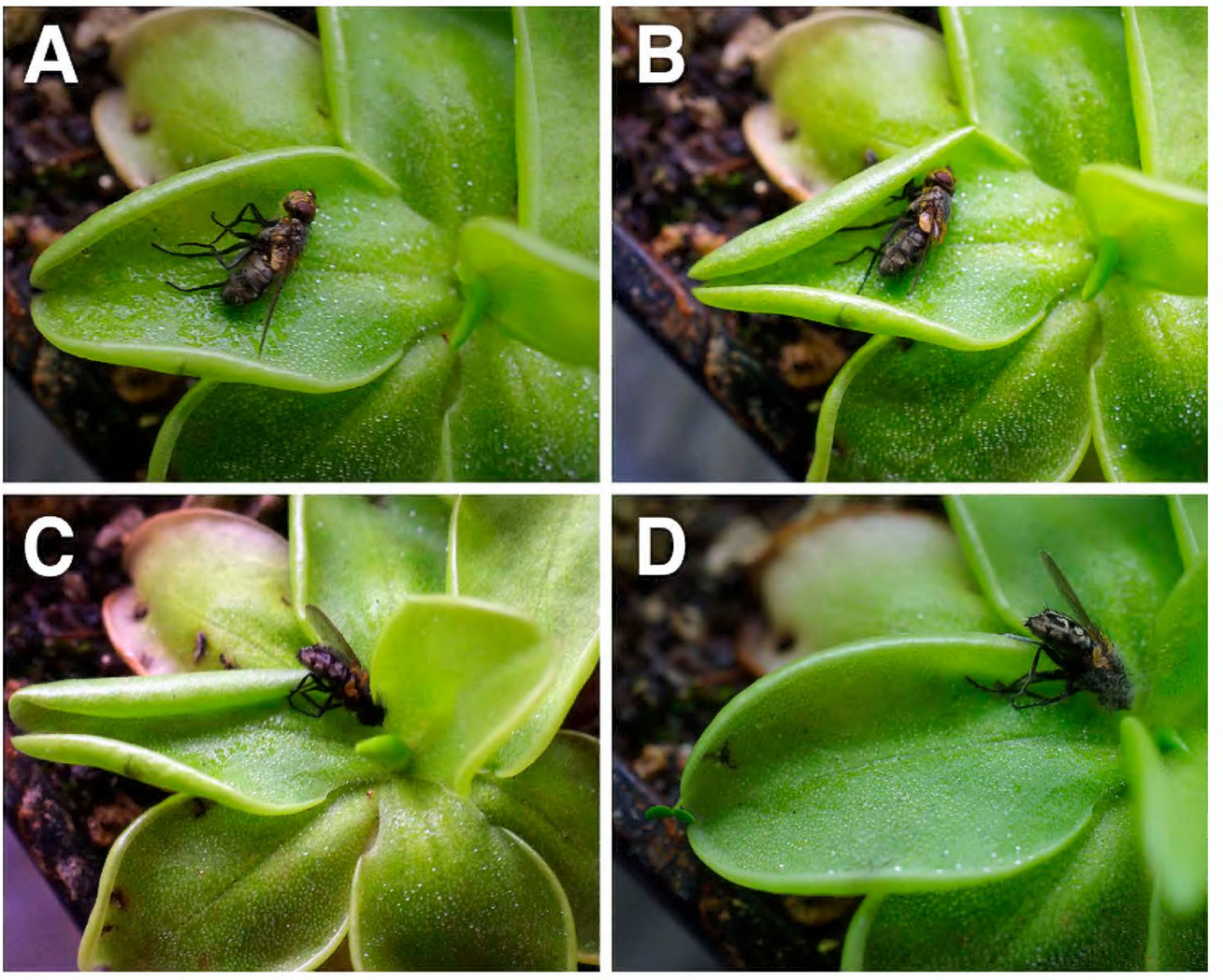

Figure 2: *Pinguicula crystallina* subsp. *hirtiflora*: (A) Time 0, food was placed. (B) Time 1 hour, leaf scrolling is obvious. (C) Time 6 hours, by joining the edges of the leaf, a carnivorous roll was created. After 24 hours the leaf began to open. (D) Time 29 hours, the leaf had returned to its original shape.

Conclusion

Both tropically homophyllous species native to Europe have movable leaf margins. They work by making their upturned leaf edges bend more and come closer together. This appears to be an adaptation to increase the absorption surface of the trap. The object of the documented endeavor is the liquid product of digestion.

The entire digestion time was 4.5 days for *P. lusitanica*, while only 1 day for *P. crystallina* subsp. *hirtiflora*. But it cannot be said that one works faster than the other. Digestion is affected by the size of the prey, its digestibility, and certainly also the condition of the plant.

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A survey of pesticide use in horticulturally-grown carnivorous plants, with a review of arthropod pests

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Abstract: Arthropod pests are sometimes reported from horticulturally-grown carnivorous plants. While it is broadly known which pest groups are involved, little work has been done to characterize them specifically, which can be important when implementing control strategies. Pesticide recommendations are available through books and other media, but pesticides have not been systematically tested for phytotoxic effects in carnivorous plants so growers may worry about using them. In response to these issues, we conducted a survey of carnivorous plant growers to understand what pests they encounter, which pesticides they use, and if any of those pesticides have caused issues to the plants, the results of which are reported herein. We also provide a summary of different arthropod pests recorded from carnivorous plants in order to provide context for these pests and their control, and to encourage growers to document pests they encounter to fill in knowledge gaps.

Introduction

Carnivorous plants are well known for their ability to consume insects and other arthropods and most popular and scientific literature about them focuses on this phenomenon (Ortuño-Mendieta *et al.* 2021; Mithöfer 2022). However, carnivorous plants can also be attacked by herbivorous arthropods. Commercial and private individuals that grow carnivorous plants are generally intolerant of pest infestations as arthropod feeding can reduce plant vigor, cause stunted or deformed leaves, which may impair the ability of plants to capture prey, kill leaves outright, reduce seed production, reduce overwintering viability, or reduce the ability to sell plants (D'Amato 1998; Hewitt-Cooper 2016).

Within popular literature, most pest groups are discussed at higher taxonomic levels such as family or superfamily, e.g., aphids or whiteflies (Hanna 1979; Lecoufle 1990; D'Amato 1998; Meyers-Rice 2001; Romanowski 2002; Hewitt-Cooper 2016; ICPS 2022a). A few works have summarized the current knowledge of arthropod herbivores associated with specific carnivorous plants (e.g., Mithöfer 2022), but there is no comprehensive list of herbivorous arthropod species associated with all carnivorous plants. Important traits, such as pesticide susceptibility or the ability to transmit plant pathogens, can vary between species and within higher groups (e.g., not all aphids can transmit all plant viruses) so this lack of detail may negatively impact pest control solutions and outcomes.

Information about pest control methods for carnivorous plants is available to growers through various resources including books, social media, and video-sharing websites. While

these sources often contain useful knowledge, they can have potential issues. For example, they can become outdated as older pesticides are phased out or when newer, safer pesticides become available, books can go out of print and become difficult to find, and internet resources can become inaccessible due to changes in individual website policies, trends in social media, users deleting content, and even changes in national and international laws (Peters 2023; Skvarla & Fisher 2023).

While pesticides are used to control pests, they can also be toxic to plants, a phenomenon known as phytotoxicity (OEPP/EPPO 2014; Sharma *et al.* 2019). Some plants are more or less sensitive to different chemicals, so pesticides that are safe for one plant may have phytotoxic effects on another (Getter 2015; Steil 2022). Temperatures above 26.6°C (80°F) and high humidity, which are the preferred growing conditions for many carnivorous plants, also increase the risk of phytotoxic effects (Getter 2015). Additionally, carnivorous plants are intolerant of minerals in their water and similar substances may be present in some pesticides as "inert ingredients" (materials included in pesticide formulations that are not the active ingredient). Therefore, growers may be concerned about whether pesticides are safe to use on carnivorous plants. Such concerns are not unfounded. One book about growing American pitcher plants (*Sarracenia* spp.) even advised that "if you must use an insecticide, do so at half strength, through even this may be enough to damage immature pitchers" (Romanowski 2002). Replicated phytotoxicity assessments are regularly conducted for pesticides applied to crops and ornamental plants, but, as far as we are aware, none have been done and reported for carnivorous plants. This is likely due to the specialty nature of carnivorous plants and their relatively small market share compared to more conventional ornamental plants.

In order to assess current trends of pesticide use among carnivorous plant growers and determine if pesticide phytotoxicity trials are warranted, we reviewed books and online information sources (e.g., YouTube, specialty websites) for information regarding pesticide recommendations. We also surveyed growers about their pest issues and pesticide use. To put this information into context, we provide a review of arthropod pests associated with carnivorous plants and indicate knowledge gaps that growers can help fill.

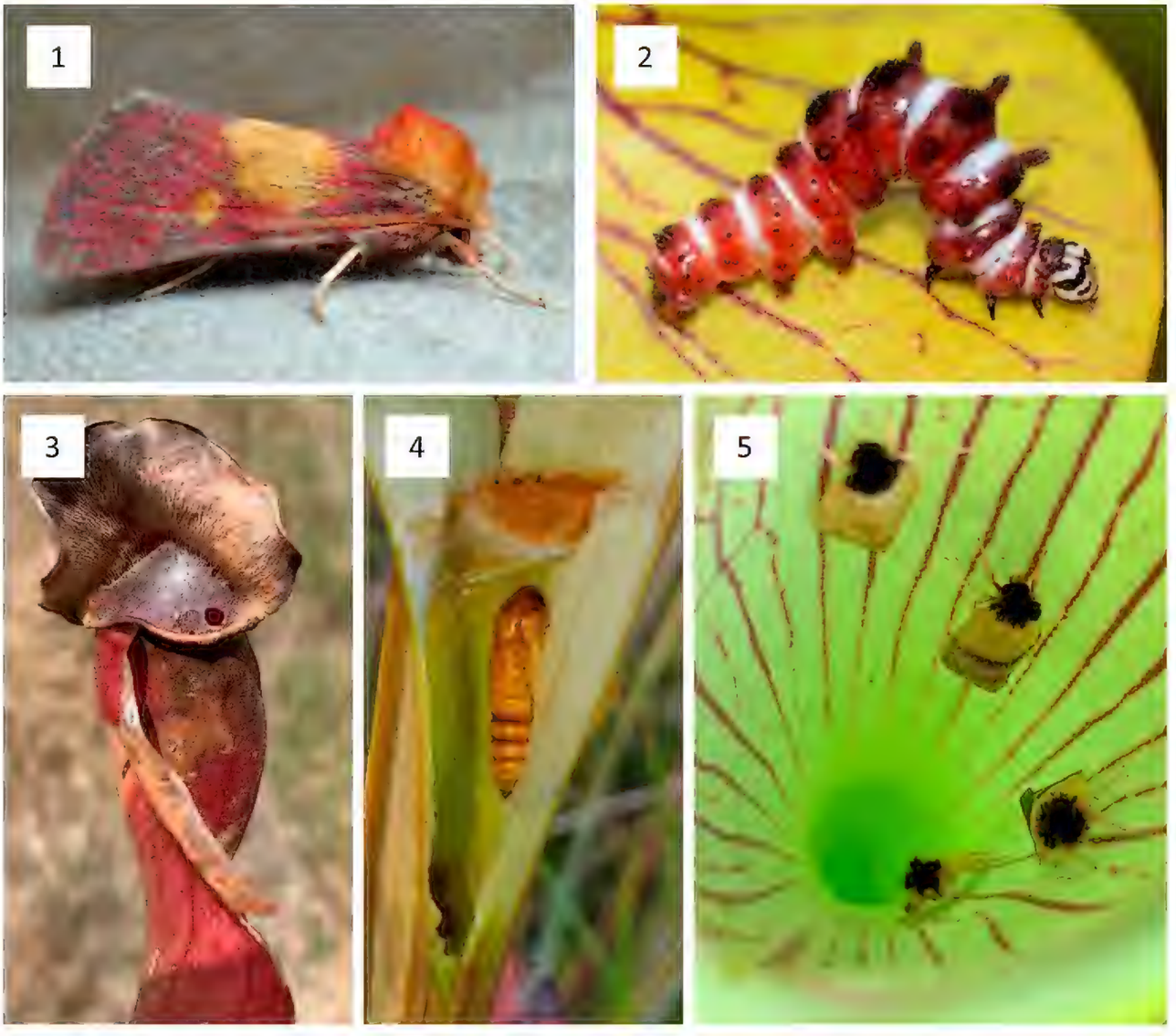
Materials and methods

Books about carnivorous plants were screened for information about arthropod pests and associated control methods. An extensive literature search was conducted using Google Scholar for scientific articles that referenced arthropods that feed on carnivorous plants. GenBank was searched for plant virus sequences (Benson *et al.* 2013). Internet searches were executed using the common or scientific names of plants (e.g., sundew or *Drosera*), arthropod groups (e.g., aphid or Aphididae), and/or "virus". Taxon-specific websites were searched for host records as well (García Morales *et al.* 2016; Blackman & Eastop 2023; Robinson *et al.* 2023; Ulitzka 2023).

A survey of carnivorous plant growers was conducted to determine which arthropod pests growers encounter, which pesticides growers have used on their plants, and if any of those pesticides have caused adverse reactions in plants. The survey was advertised on multiple carnivorous plant Facebook groups and on Reddit through the r/SavageGarden subreddit in early February 2023. It was also sent directly to a few commercial nurseries located in the United States, although personally identifiable information was not gathered and it could not be assessed whether the nurseries responded to the survey or not. The survey was approved by the Pennsylvania State University Internal Review Board (STUDY00021775).

Pest Review

Chewing pests. This group includes a variety of herbivorous arthropods that chew on plants, including various caterpillars and beetles. They are best studied in American pitcher plants (*Sarracenia* spp.), which host three species of pitcher plant moths: *Exyra fax*, which specializes on *S. purpurea* (Fig. 1), *E. ridingsii*, which feeds on *S. flava* and sometimes *S. minor*, and *E. semicrocea*, which feeds on all *Sarracenia* species, although it is less common in *S. purpurea* and *S. psittacina* (Jones 1907, 1921; Folkerts & Folkerts 1996; Schnell 2002; McPhearson & Schnell 2011). Folkerts and Folkerts (1996) provided identification keys to *Exyra* caterpillars, adults, and feeding damage. As



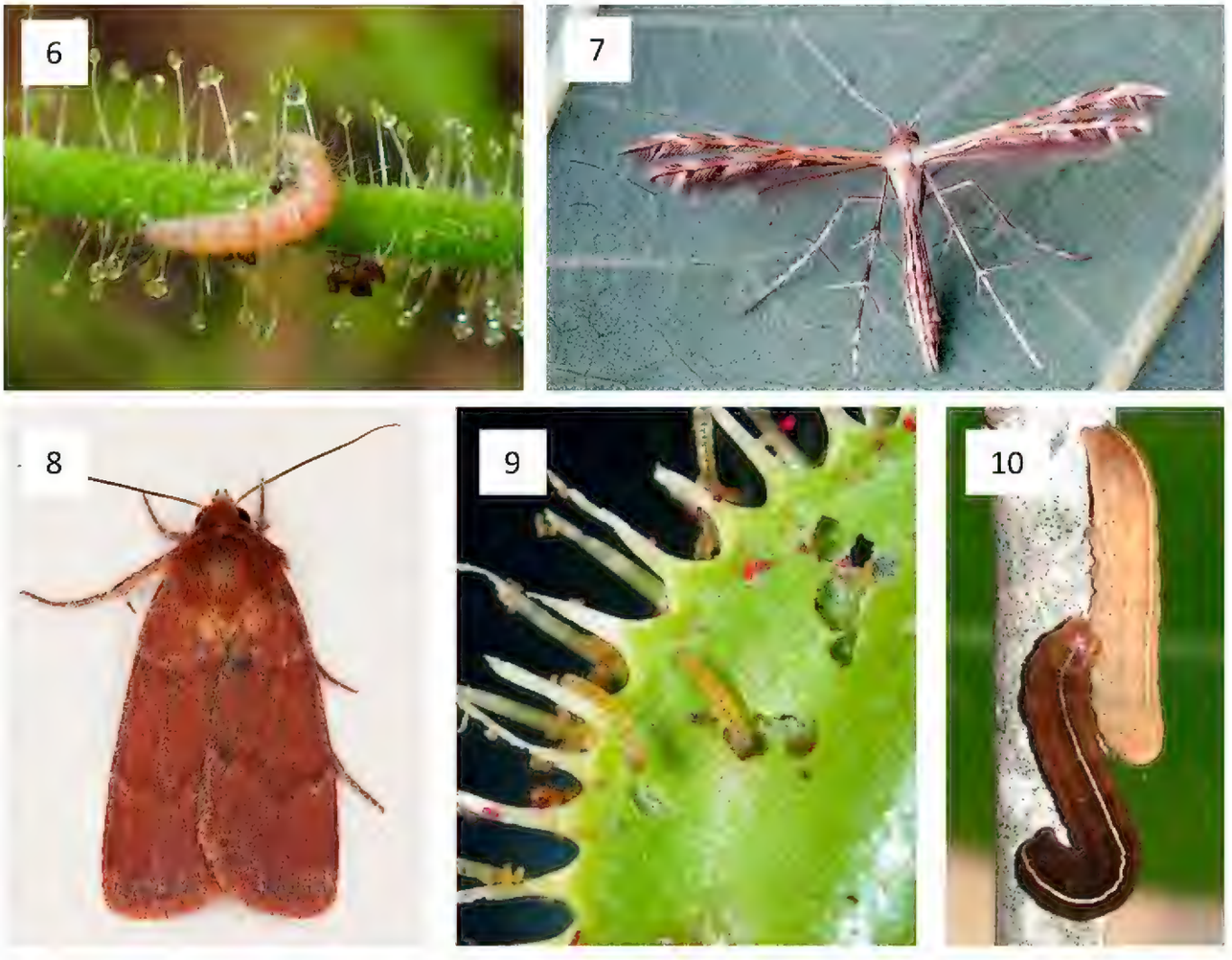
Figures 1–5: Pitcher plant moths. (1) Adult *Exyra fax*. (2) *E. semicrocea* caterpillar. (3) *Sarracenia purpurea* pitcher colonized by *E. fax*. Note the damaged tissue and webbed up pitcher opening. (4) *Exyra* pupa inside of a dissected *Sarracenia* pitcher. (5) Adult *E. semicrocea* sheltering within a *Sarracenia* pitcher. Figures 1, 2, 3, and 5 by Chris Buelow, Ashley Bosarge, Paul Dennehy, and Chrisaggie, respectively, via iNaturalist, used under CC BY-NC 4.0 Deed licenses. Figure 4 by Laura Gaudette via iNaturalist, used under a CC BY 4.0 Deed license.

caterpillars, these moths feed inside *Sarracenia* pitchers (Fig. 2, Front Cover). This causes direct damage via tissue loss but also causes the pitchers to fall over and prevents them from trapping prey (Fig. 3, Back Cover). Pupae develop within the pitchers they feed on and adult moths are also often found inside of the pitchers (Figs. 4–5). Most studies have found that caterpillar feeding negatively impacts plant growth and size (Atwater *et al.* 2006; Moon *et al.* 2008; Carmickle & Horner 2019), although one found that it did not (Ricci *et al.* 2017). More than 80% of pitchers at a site can be colonized by *Exyra* moths, so their impact is not inconsequential where they occur (Moon *et al.* 2010; Carmickle & Horner 2019). Two polyphagous moth species, *Choristoneura parallela* and *Morrisonia confusa*, also feed on *Sarracenia* pitchers (Jones 1908; Lamb & Kalies 2020). Jones (1908) reported that "larvae [of *C. parallela*] of different ages were found in localities widely separated, so their occurrence in this food-plant was evidently not accidental", while in contrast *M. confusa* has only been found on *Sarracenia* once. Beyond the pitchers, the bagworms *Basicladus tracyi* feed on the flower petals and *Endothenia hebesana* feed on the developing seeds (Jones 1908, 1911; Romanowski 2002; Schnell 2002). Southern *E. hebesana* pupate in the flower while northern individuals bore into the flower stalk, so Folkerts (1999) suggested that the species *E. daeckeana* may need to be resurrected for the northern population. These flower- and seed-feeding species do not impact the overall health of individual plants, but *Endothenia* feeding can significantly reduce seed yield. This does not impact natural regeneration in wild *Sarracenia* populations (Rymal & Folkerts 1982; Folkerts 1992; USFW 1994) but could be of concern to growers producing *Sarracenia* seed.

Tropical pitcher plants (*Nepenthes* spp.) are well defended chemically by various secondary metabolites and also fibrous tissue in the leaves and stems, so few herbivorous insects feed on them (Tan *et al.* 2020). Two species are known to feed on *N. bicalcarata*: a weevil (*Alcidodes* sp.) that feeds on young pitchers and prevents them from maturing into prey-capturing organs (Merbach *et al.* 2007) and a butterfly larva (species unknown) bores a hole in young pitchers just before they open, which causes digestive fluid to drain out and allows the caterpillar to feed on the empty pitcher (Clarke 1997). Another moth, *Eublemma radda*, has been recorded on *N. bicalcarata*, *N. gracilis*, *N. mirabilis*, and *N. rafflesiana* but the relationship is less detrimental (Beaver 1983; Clarke 1998). The caterpillars live in and graze on the inside wall of *Nepenthes* pitchers, which causes clear windows to appear. Damaged pitchers will collapse after a few weeks, although the pitchers seem to function for just as long as uncolonized pitchers so the effect on prey capture and plant health may be negligible (Clarke 1997, 1998). Similarly, *Phyllocnistis nepenthae* caterpillars mine the pitchers but this does not affect prey capture or pitcher longevity (Tan *et al.* 2020). Generalist caterpillars have been noted to feed on *Nepenthes* leaves, including tussock moths and bagworms, but these cause localized and minimal damage (Hewitt-Cooper 2016; Tan *et al.* 2020). African cotton leafworm (*Spodoptera littoralis*) caterpillars that were experimentally fed *Nepenthes* leaves did not grow (Dávila-Lara *et al.* 2021; Rahman-Soad *et al.* 2021), so herbivory by non-specialists on *Nepenthes* is likely self-limiting and not much of a concern to growers. Pitcher blue butterflies (*Deudorix kessuma*), which are native to southeast Asia, are specialists on *Nepenthes* seed pods (Tan *et al.* 2020). Florida pink scavenger moths (*Anatrachyntis badia*), which are generalist seed feeders found it in Southeast United States and California, have also been recorded on *Nepenthes* seed pods (Tan *et al.* 2020). Neither species affects the overall health of infested plants but may reduce seed production.

Sundews (*Drosera* spp.) are fed upon by the caterpillars of a few moth groups. The genus *Buckleria* includes six species, three of which are known to feed on sundews (Figs. 6–7; Table 1).

Buckleria caterpillars avoid becoming trapped by sticky glandular hairs of sundews by licking the mucilage off the hairs, thus rendering the trap safe, before consuming the leaf (Osaki & Tagawa 2020). The caterpillars also feed on the flowers and flower stalk and it has been hypothesized that rapid flower closure in response to mechanical stimuli exhibited by some sundews may be a defense against *Buckleria* feeding (Matthews 2009; Tagawa *et al.* 2018). Herbivory damage by *Buckleria* in some areas can be high (Kataoka & Nishimoto 2007). Sundew dart moths (*Hemipachnobia monochromatea*) are found in Northeastern North America west to Alberta (Fig. 8). Early instars feed on sundews while later instars can host switch onto cranberry, blueberry, and sheep laurel (Hooker 1919; Wagner 2011; MPG 2023; Robinson *et al.* 2023), but they have otherwise been little investigated. Carnation tortrix (*Cacoecimorpha pronubana*) are highly polyphagous moths native to the Mediterranean region that were first recorded in the United Kingdom around 100 years ago. In 2012, they were found feeding on nursery-grown Cape sundews (*D. capensis*) in Essex, U.K, so this is an interesting interaction where neither the host plant nor the herbivore are native to the region where they were found to interact (Signorile 2012). *Spodoptera apertura* are found in Africa,



Figures 6–10: Lepidoptera that feed on carnivorous plants. (6) European sundew moth (*Buckleria paludum*) caterpillar feeding on *Drosera*. (7) *B. paludum* adult. (8) Adult sundew dart moth. (9) Early instar and (10) mature Venus flytrap moth caterpillars. Figure 6 by Hugo Innes via iNaturalist, used under a CC BY 4.0 Deed license. Figures 7 and 8 by Cossus and Michael H. King, respectively, via iNaturalist, used under CC BY-NC 4.0 Deed licenses. Figures 9 and 10 by Bo Sullivan, used with permission.

Australia, and southeast Asia and have been reported to feed on tobacco (*Nicotiana*) but also on *Drosera* in India (Sevastopulo 1941; Robinson *et al.* 2023).

Venus flytraps (*Dionaea muscipula*) host Venus flytrap cutworm moths (*Hemipachnobia subporphyrea*) (Figs. 9–10). This species was described in the late 1700's but not observed again until 1974, when it was rediscovered in North Carolina. Since then, only five additional populations have been found, with five total populations in North Carolina and one in Maryland (Hall & Sullivan 2000; Hall *et al.* 2023). One survey found that Venus flytraps at ten additional sites had feeding damage characteristic of *H. subporphyrea*, but their presence has not been confirmed by finding larvae or adults (Hall & Sullivan 2006). In fact, only a handful of adult specimens have ever been collected (24 as of 2000; Hall & Sullivan 2000). Caterpillars have been found on commercial Venus flytraps cultivated in semi-natural conditions, where they produced extensive damage in 1986, but have only recently been observed in the wild (Hall & Sullivan 2000; Hall pers. comm.). A population in Maryland exists where Venus flytraps do not occur and lab-reared caterpillars successfully fed on sundews and a later instar caterpillar fed on creeping blueberry (*Vaccinium crassifolium*), so

Table 1. Information about *Buckleria* species, including associated host plants.

Species	Plant hosts	Range	Year described	References
Buckleria brasilia	*Drosera graminifolia*	Brazil	2006	Gielis 2006
Buckleria girardi		central and western Africa	1992	Gibeaux 1992; De Prins & De Prins 2021
Buckleria madecassea		Madagascar	1994	Gibeaux 1994; De Prins & De Prins 2021
Buckleria negotiosus		South Africa, Zimbabwe	1926	Meyrick 1926; Gielis 2008; De Prins & De Prins 2021
Buckleria paludum	*D. burmanni*, *D. rotundifolia*, *D. serpens**, *D. spatulata*	Europe, Asia, Australia	1841	Ustjuzhanin & Kovtunovich 2017; Tagawa *et al.* 2018; Osaki & Tagawa 2020; Robinson *et al.* 2023
Buckleria parvulus	*D. brevifolia*, *D. filiformis*, *D. tracyi*	eastern United States, primarily the southern coastal plain	1921	Matthews 2009
Trichoptilus scythrodes‡	*D. peltata* complex	Australia	1886	ALA 2023a, b; Hobern 2020, 2021, pers. comm. 2023

* Tagawa *et al.* (2018) reported *B. paludum* from *D. toyoakensis*, which Schlauer *et al.* (2019) synonymized with *D. serpens*. That change is reflected here.

‡ According to Donald Hobern, *Trichoptilus scythrodes* has male genitalia that are similar to *B. paludum* and has a COI barcode sequence that is 6% different from that species, so should be transferred to *Buckleria* as *B. scythrodes*. As a formal transfer has not been published, we retain it within *Trichoptilus* here but include it in the table as we expect it will be moved in the future.

they may host switch like the closely related sundew dart (see above). However, in North Carolina, Venus flytrap cutworm moths have not been found in areas that support only sundews but not Venus flytraps, so Venus flytraps are likely a necessary host in that state (Hall *et al.* 2023). The species is globally rare and one of the most imperiled insects in North America, although the U.S. federal government and other international agencies (e.g., the International Union for Conservation of Nature) have not recognized it as endangered so it has few formal protections. Due to their scarcity and limited range, Venus flytrap cutworms are not an issue for most growers.

Butterworts (*Pinguicula* spp.) in Mexico are eaten by pyrgomorphid grasshoppers (species not reported) and terrestrial mollusks. Most plants (74.3%) had low-levels of herbivore damage (0.5-3% of total leaf area), although some individual plants lost up to 40% of the total leaf area (Alcalá *et al.* 2010; Ortuño-Mendieta *et al.* 2021). Chewing herbivores have not been reported from wild butterworts elsewhere in the world, although slugs are reported to feed on cultivated butterworts in popular literature (Hewitt-Cooper 2016).

Root-boring insects attack the rhizomes of pitcher plants. Perhaps the best known are pitcher plant borer moths (*Papaipema appassionata*) (Figs. 11–12). While this species occurs throughout eastern North America, they are most common and abundant in the Great Lakes region (Lamb & Kalies 2020). Pitcher plant borer moths feed on *Sarracenia purpurea* throughout their range and have also been found on *S. alata*, *S. flava*, and *S. rubra* in the Southeast (Jones 1908; Schnell 2002; Brou 2005; Lamb & Kalies 2020). As the caterpillars bore through pitcher plant rhizomes, orange-brown excrement builds up around the base of the plant and indicates an infestation. The boring damage can be extensive and result in wilting pitchers and plant death (Jones 1908; Kalies 2020).

Black vine weevils (*Otiorhynchus sulcatus*) (Figs. 13–14) are another root-feeding pest that attack *Sarracenia* and *Darlingtonia* (Rice 2001). This species is native to Europe but was introduced to North America by 1831, where it is now widespread. It has also been introduced into New Zealand, mainland Australia and Tasmania, Japan, and Chile (Moorhouse *et al.* 1992). Young black vine weevil larvae feed on fine roots, while older larvae bore through the roots themselves. When

Figures 11–14: Root-boring pests that feed on pitcher plants. (11) Pitcher plant borer moth caterpillar in a *Sarracenia* rhizome and (12) an adult moth. (13) Black vine weevil larva and (14) adult. Figure 11 by Teá Montagna via iNaturalist, used under CC BY 4.0 Deed license. Figures 12 and 14 by Denis Doucet and David Cappaert, respectively, via iNaturalist, used under a CC BY-NC 4.0 Deed license. Figure 13 by Peggy Greb, USDA Agricultural Research Service, via Bugwood.org, used under a CC BY 3.0 US Deed license.

they feed on pitcher plant rhizomes, this can cause wilting pitchers and kill infested plants. The preferred larval hosts include the roots of yews (*Taxus* spp.) and rhododendron (*Rhododendron* spp.), but black vine weevils are relatively polyphagous and have been recorded from 150 species of plants (Moorhouse *et al.* 1992). During experimental feeding trials, weevil larvae fed on 101 of 108 offered hosts (Masaki *et al.* 1984), so the potential host range is likely larger than currently known. While they have not been recorded from carnivorous plants, other *Otiorhynchus* species are also polyphagous root-feeders that have been spread around the world through commercial horticulture, so may be pests on pitcher plant rhizomes if given the opportunity.

Adult *Otiorhynchus* weevils are nocturnal and feed on plant leaves at night, which produces a characteristic notching along leaf edges. While this feeding is rarely heavy enough to stress the plant, it can help identify an infestation of larvae in the roots, which might otherwise be missed until the plant dies. Female weevils are flightless and are usually introduced into a new area through infested plants, so inspecting new plants before incorporating them into the landscape can help prevent infestations. Keeping pitcher plants in water baths and eliminating bridges across the water (e.g., sticks, fallen pitchers) will help keep weevils out of potted pitcher plants if they are already present in the landscape. Once weevils are established in the rhizome, manually removing them can be effective. Entomopathogenic nematodes (*Steinernema* and *Heterorhabditis* spp.) are commercially available and can control weevil larvae but may be slow to produce results. Biorational pesticides such as *Bacillus thuringiensis gallariae* (Btg) can be applied when adults are present to kill them when they feed on plant leaves. Imidacloprid applied as a soil drench is effective against larvae, but other broad-spectrum insecticides such as carbaryl and malathion are not (Frank *et al.* 2020a).

Sucking pests include a variety of groups, such as true bugs like scale insects and aphids, as well as thrips and even arachnids like spider mites. Different groups feed on the phloem, xylem, or contents in individual plant cells, so pesticides can have variable control depending on the pest group, how the pesticide is applied, and the pesticide mode of action. Signs and damage vary by pest, but often consist of stunted plant growth; leaf curling, yellowing, browning, or stippling; and the production of honeydew and the associated growth of sooty mold.

Aphids are soft-bodied true bugs that feed on plant phloem using piercing-sucking mouthparts (Figs. 15–16). They are mostly a northern temperate group and are not well represented in tropical regions (Blackman & Eastop 2023). While more than 5,700 species occur worldwide (Favret 2023), fewer than 300 are considered serious pests. Aphids have been reported from *Cephalotus*, *Dionaea*, *Drosera*, *Drosophyllum*, *Genlisea*, *Heliamphora*, *Nepenthes*, *Pinguicula*, *Sarracenia*, and *Utricularia* in popular literature (Lecoufle 1990; D'Amato 1998; Fleischmann 2012; ICPS 2022). However, only a few have been identified to species from a limited number of carnivorous plant hosts in the scientific literature (Table 2).

Aphid feeding can cause direct damage to plants, which often manifests in carnivorous plants as twisted or stunted leaves (D'Amato 1998; Hewitt-Cooper 2016). They also produce honeydew, which is a sugary waste product that can grow black sooty mold. However, in most horticultural and agricultural systems, the majority of damage associated with aphids is due to the plant pathogens they vector rather than direct feeding damage (Dedryver *et al.* 2010). Carnivorous plants are not agronomically valuable so have not been systemically surveyed for plant pathogens (Miguel *et al.* 2016). In consequence, only a few aphid-vectored pathogens are known from them (Table 3). Of these, both *Cucumber mosaic virus* and *Beet western yellows virus* have wide host ranges (1200 and 150 species, respectively; Zitter & Murphy 2009, Yoshida & Tamada

Figures 15–18: Aphids and aphid-vectored virus damage in carnivorous plants. (15) Aphids feeding on a *Drosera rotundifolia* flower stalk. (16) Aphid mummies on a *Sarracenia* pitcher. Mummies are made by parasitoid wasps and indicate that beneficial biocontrol agents are attacking the aphids. When mummies are present, broad-spectrum pesticides should be avoided. (17) Discoloration on a *Sarracenia* phyllodia and (18) pitcher caused by *Cucumber mosaic virus*. Figure 15 by Tero Karppinen via Flickr, used under a CC BY 2.0 Deed license. Figure 16 by u/Plutoniumburrito via reddit, used with permission. Figures 17 and 18 by Adam Gaupp via The Sarracenia Forum, used with permission.

2019), so finding them in carnivorous plants is perhaps not surprising (Figs. 17–18). These widespread viruses have only been reported from carnivorous plants in two and one locality, respectively, but it's not clear if the lack of reports is due to a lack of survey effort or because they rarely infect carnivorous plants.

Scale insects includes a number of related groups, including hard scales (Diaspididae), soft scales (Coccidae), and felt scales (Eriococcidae). They all feed on plant liquids using piercing-sucking mouthparts, lack wings (except for adult males), and are often treated as a single group in popular literature. However, there are important differences between them that can impact control solutions when infestations occur.

Hard scales are sedentary insects that do not move after they settle down to start feeding. Most life stages are covered by a hard wax scale or test, which protects them from natural enemies, adverse weather, and pesticides. Only the crawlers, which are the youngest stage that hatches from the eggs, lack a waxy test and can move. Because they are so small, crawlers can move from plant to plant by being blown about on the wind, being moved by birds, or crawling from nearby

Table 2. Aphid species recorded from carnivorous plants.

Species	**Plant hosts**	**Carnivorous plant hosts**	**Geographic range of aphid**	**Area recorded from CPs**	**References**
Aphis droserae	*Drosera*	*Drosera loureirii*, *D. peltata*, *D. rotundifolia*	China, Taiwan, Germany	China, Taiwan, Germany	Takahashi 1921; Tao 1991; Barjadze *et al.* 2017; Blackman & Eastop 2022
Aphis franeulae sensu lato	varies by subspecies, including *Epilobium angustifolium*, *Capsella bursa-pastoris*, *Lysimachia vulgaris*, *veronica beccabunga*	*Drosera rotundifolia*	Cosmopolitan	Germany	Müller 1978
Aphis nasturtii	Polyphagous	*Drosera intermedia*, *D. rotundifolia*	Cosmopolitan except Australasia	Germany, Switzerland	Müller 1978; Lampel & Tinguely 1998; Holman 2008; Blackman & Eastop 2022
Aphis triglochinis	Polyphagous on aquatic/semi-aquatic plants	*Drosera anglica*, *D. intermedia*, *D. rotundifolia*	Northern, Central, and Eastern Europe, northern Asia, possibly Japan	Germany, Great Britain, Latvia, The Netherlands, Sweden	Holman 2008; Blackman & Eastop 2022
Cavariella aegopodii	Usual hosts are various Apiaceae	*Drosera rotundifolia*	Cosmopolitan	Germany	Müller 1987; Holman 2008
Aulacorthus solani	Polyphagous	*Sarracenia purpurea*	Cosmopolitan	The Netherlands	Piron 2017; Blackman & Eastop 2022

Table 2. Continued

Species	Plant hosts	Carnivorous plant hosts	Geographic range of aphid	Area recorded from CPs	References
Hyalomyzus jussiaeae	Usual host is *Ludwigia* but may colonize other aquatic/ semi-aquatic plants	*Drosera capilaris*	Eastern North America and Central America	Florida	Nielsson & Habeck 1971; Blackman & Eastop 2022
Macrosiphum jeanae	*Sarracenia*	*Sarracenia purpurea*	Manitoba	Manitoba	Robison 1972; Blackman & Eastop 2022
Macrosiphum sp. near *jeanae*	*Darlingtonia*	*Darlingtonia californica*	California	California	Nielsen 1990; Blackman & Eastop 2022
Myzus lytheri	Usual host is *Lythrum* but may colonize other aquatic/ semi-aquatic plants	*Drosera rotundifolia*	Europe, Africa, central Asia, North America	Poland	Szelegiewicz 1966, 1968; Holman 2008; Blackman & Eastop 2022
Neomyzus circumflexus	Polyphagous	*Sarracenia purpurea*	Cosmopolitan	The Netherlands	Piron 2017; Blackman & Eastop 2022
Rhopalosiphum nymphaeae	Polyphagous on aquatic/semi-aquatic plants	*Drosera anglica*, *Utricularia*	Cosmopolitan	Czech Republic	Homan 1991, 2008; Blackman & Eastop 2022

infested plants. Hard scale feeding can result in weakened and stunted plants, yellowing or discolored leaves, or even plant death. Unlike many other plant-feeding insects with piercing-sucking mouthparts, hard scales do not feed on sap from the phloem. Rather, they rupture individual plant cells and consume the contents. This makes control using systemic insecticides difficult as insecticides are usually not translocated into the cells where scales feed. So foliar insecticides are applied when the crawlers are present. Different hard scale species may be univoltine (one generation

Table 3. Aphid-vectored plant viruses reported from carnivorous plants.

Virus	Plant host	Reported from	Reference
Beet western yellows virus	*Nepenthes mirabilis*	France	Miguel *et al.* 2016
Cucumber mosaic virus	*Sarracenia* sp.	Germany	GenBank accession number MW582807.1
Sarracenia purpurea virus	*Sarracenia purpurea*	Germany	Barckhaus & Weinert 1975; Jackson *et al.* 2008
Turnip mosaic virus	*Utricularia* sp.		GenBank accession number AB701736.1

per year) or multivoltine (multiple generations per year) and crawlers may be present at different times of the year, so identifying hard scales to species can be important for timing control measures. Dentate scale (*Velataspis dentata*) and false oleander scale (*Pseudaulacaspis cockerelli*) (Fig. 19), both of which are polyphagous and have broad host ranges, have been recorded from *Sarracenia purpurea* in Georgia (Tippins 1968; Beshear *et al.* 1973). *Chrysomphalus nepenthivorus* are only known from specimens that were intercepted in the United States on "several hybrids of *Nepenthes*" exported from Thailand (Smith-Pardo *et al.* 2012). Hard scales that occur on *Nepenthes* elsewhere in the world are likely polyphagous pest species, but none have yet been identified to species. Hard scales have also been reported from *Darlingtonia*, *Dionaea*, and *Genlisea*, but the species on these hosts are unknown (Lecoufle 1990; Fleischmann 2012) (Fig. 20).

Soft scales are somewhat similar in appearance to hard scales but are more variable. Some species are flat and lack a waxy covering while others are highly rounded; some species have legs and can move while others lack legs after the crawler stage; and some species are similar in size to hard scales while others are larger and more conspicuous. Unlike hard scales, soft scales feed in the phloem and produce honeydew like aphids. A number of polyphagous species are important pests in greenhouses and on indoor plants. Nigra scale (*Parasaissetia nigra*), a polyphagous species known from more than 400 plant hosts (Fig. 21), has been collected from greenhouse-grown *Nepenthes* in South Africa (Krüger & Douglas-Smit 2013). A specimen of Florida wax scale (*Ceroplastes floridensis*), which occur throughout the Southeastern United States, was collected on *Sarracenia minor* from an unknown location in 1876 (Gimpel *et al.* 1974). Finally, a photograph of what appears to be brown soft scales (*Coccus hesperidum*, Fig. 22) on *Heliamphora* was published by Hewitt-Cooper (2016).

Felt scales are similar in appearance to mealybugs but are not covered in as much wax, so that most of the pink, red, purple, or green body can be seen. All life stages have legs and are capable of moving. Most species are feed on a limited host range and a few are important pests of ornamental plants (Skvarla & Schneider 2022). The only felt scale known to feed on carnivorous plants is *Acanthococcus droserae*, which has been collected from wild sundews in Florida and Georgia (Miller *et al.* 1992). Felt scales feed on sap in the phloem (Wu *et al.* 2022), so in the unlikely event that they become pests on cultivated sundews in the Southeastern United States, systemic insecticides should control them.

Figures 19–27: Examples of sucking pests that feed on carnivorous plants. (19) False oleander scale infestation on a non-carnivorous plant. (20) Hard scales on a *Dionaea muscipula* trap. No scale species have been documented from Venus flytraps, so this is likely a new, undescribed host association. (21) Nigra scale infestation on a non-carnivorous plant. (22) Brown soft scales are among the most important soft scale species in greenhouses. (23) Obscure mealybugs, (24) greenhouse whiteflies, (25) western flower thrips, and (26) two-spotted spider mites are polyphagous pests of many different plant species that can be especially problematic on plants grown in indoor settings. (26) Individual two-spotted spider mites are small and difficult to see, but infestations can create large amounts of webbing that covers a plant. Figures 19, 21, 22, and 23 by Matt, donnamareetomkinson, bikingbirder, and James Bailey respectively, via iNaturalist, used under CC BY-NC 4.0 Deed licenses. Figure 20 by Ro Ja via Facebook, used with permission. Figures 24 and 27 by Whitney Cranshaw, Colorado State University, via Bugwood.org, used under a CC BY 3.0 US Deed. Figure 25 and 26 by David Cappaert via Bugwood.org, used under a CC BY-NC 3.0 US Deed license.

Mealybugs are small, slow-moving, soft-bodied insects that are covered in soft waxy filaments. Like aphids and soft scale insects, they feed on plant sap via the phloem. Mealybug feeding can weaken plants and cause stunting and malformed leaves. They also produce honeydew, which can result in the growth of sooty mold. While mealybugs can be pests on outdoor plants, they are often well controlled by natural enemies that prey on and parasitize them. A number of species are pests in greenhouses and on indoor plants, where they can escape the pressure of natural enemies. Obscure mealybugs (*Pseudococcus viburni*) are a polyphagous pest species that have been recorded from *Nepenthes mirabilis* and *Sarracenia purpurea* in the scientific literature (Ben-Dov 1994; Gimpel & Miller 1996) (Fig. 23). Growers have also noted mealybugs on *Darlingtonia*, *Drosera*, *Heliamphora*, and *Nepenthes* (Lecoufle 1990; ICPS 2022; CPN 2023), although the species involved are unknown. It is likely that polyphagous species can feed on most carnivorous plants so other host genera may be at risk. Mealybugs like to squeeze into tight spaces at the bases of leaves and between other plant parts and are somewhat protected by their waxy covering, so foliar insecticides may not always provide adequate control but systemic insecticides often do.

Whiteflies are small (1–3 mm) true bugs with piercing-sucking mouthparts related to aphids and scale insects (Fig. 24). Like scale insects, newly hatched whiteflies are mobile while older immature are immobile once they settle down in a spot. Whitefly "pupae" appear as round, shiny black objects that are often fringed with wax. Adult whiteflies are small, white, and active. They fly up from the host plant when disturbed but are poor fliers so settle back onto the plant quickly. Whiteflies are often well controlled by natural enemies on outdoor plants but, like aphids, the population can sometimes grow to damaging levels before natural enemies bring it down again. Whitefly population growth is often worse on indoors plants or in protected culture where natural enemies may not exist. Whiteflies feed on sap, so damage manifests as yellowing or dying leaves and stunted growth. They also produce honeydew, which can result in the growth of sooty mold. Some species vector plant-pathogenic viruses (Fiallo-Olivé *et al.* 2020), although none of the viruses are known to infect carnivorous plants. No whiteflies have been recorded from carnivorous plants in scientific literature. They are rarely mentioned in popular sources, although they have been reported to feed on *Pinguicula* (ICPS 2022).

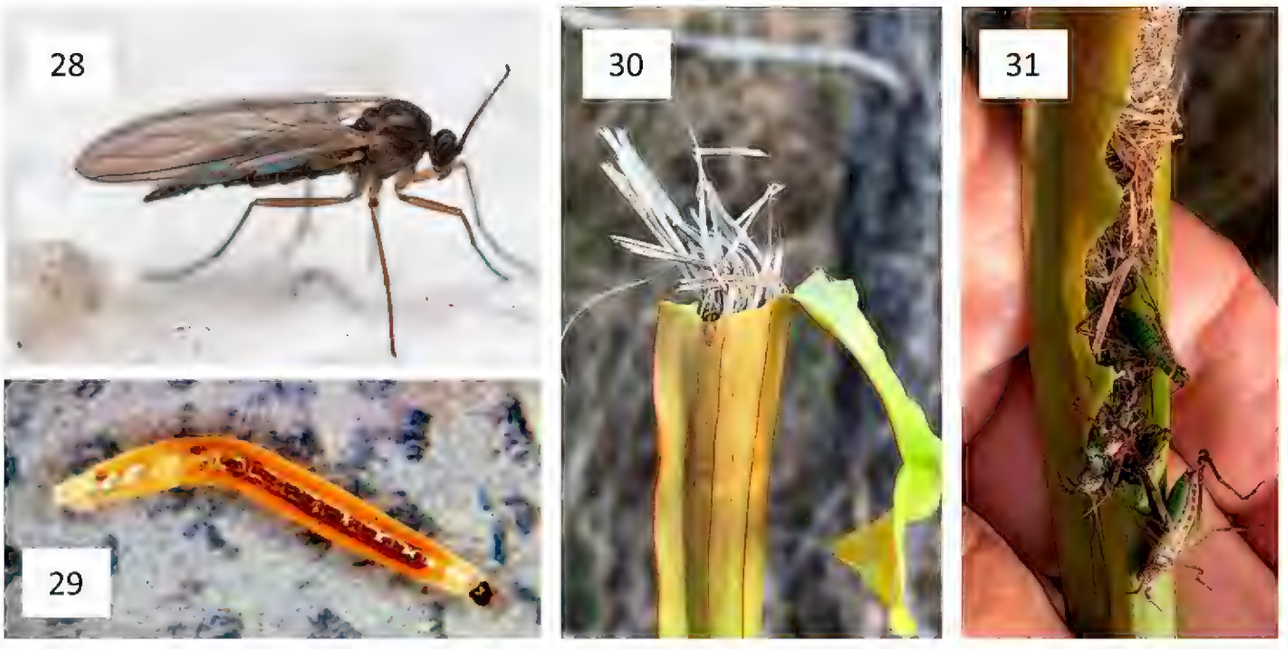
Thrips are small (0.5–14 mm, most <5 mm), elongate insects that can be a variety of colors including yellow, orange, red, black, and black with white stripes. Adults have strap-like wings covered in a fringe of hairs and can fly, while immatures lack wings and may be different colors than adults. More than half of the 6200 thrips species found worldwide feed on fungi, pollen, or other insects so are either innocuous or are beneficial pollinators and predators. In fact, while most butterworts are pollinated by other insect groups, *Thrips meridionalis* are important pollinators of *Pinguicula vallisneriifolia* (Zamora 1999; Lustofin *et al.* 2020). Although the remaining thrips species feed on plant tissue, less than 1% are considered pests (Kawale 2021). While some pest species have a narrow host range, others are extremely polyphagous. For example, western flower thrips (*Frankliniella occidentalis*) have been recorded to feed on more than 250 host plants and their full host range is likely much broader (Fig. 25). (Reitz *et al.* 2020). Regardless of the food source, thrips feed using the "punch and suck" method where they push their mouth cone into the food and suck out the contents. Plant-feeding species feed on individual plant cells, so feeding damage generally appears as stippling on leaf and flower surfaces but extensive damage may appear as large, silvery patches. Thrips may also leave behind black frass droplets that resemble drops of motor oil or varnish on plants leaves. In addition to direct feeding damage, western flower thrips and a handful of other species transmit various *Tospovirus*

species, including *Tomato spotted wilt virus*, which has a host range of nearly 2000 plant species and has caused numerous epidemics in various horticultural and floricultural crops worldwide (Parrella *et al.* 2003; Riley *et al.* 2011). *Tomato spotted wilt virus* has not been recorded from carnivorous plants but, similar to aphid-vectored plant pathogens, this is likely due to a lack of surveillance rather than an inability to infect carnivorous plants. Similarly, thrips in general have been noted to feed on *Darlingtonia*, *Nepenthes*, and *Sarracenia* (D'Amato 1998; Hewitt-Cooper 2016) but no thrips species in particular have been record from carnivorous plants. This is partly due to the difficulty in identifying thrips to species. While guides to commonly encountered species (e.g., Hodges *et al.* 2009; Bethke *et al.* 2014) can help narrow down possible identifications, thrips can only be reliably identified after being mounted on a slide and examined under a microscope by an expert.

Spider mites are small (<1 mm) plant-feeding mites that are red, green, or translucent in color (Fig. 26). Despite their small size, they are often visible with the naked eye due to their color contrasting with the infested plant. Under optimal conditions, spider mites can mature from egg to adult in five to twenty days, so populations can often explode quickly (Fasulo & Denmark 2009). Spider mites suck the contents out of individual plant cells, which kills the cells. Damage appears as stippling or bleaching and badly damaged leaves will eventually turn yellow, bronze, or grey. Spider mites also spin silk webbing over host plants, which can become extensive when infestations are large and indicate an infestation (Fig. 27). Two-spotted spider mites (*Tetranychus urticae*), which are the most important polyphagous pest species, reproduce best under hot, dry conditions so are the biggest issue outdoors during the summer and fall. However, outdoors they are often well controlled by a variety of natural enemies and dislike the humid conditions of a bog garden. Indoors, spider mites can occur year-round and can be difficult to control as there are no natural enemies present to help control them. This dynamic is reflected in the survey results, where all ten reports of spider mites were from indoor plants and there were no reports of spider mites affecting outdoor plants. Spider mites have specifically been reported from *Dionaea*, *Nepenthes*, and *Sarracenia* (Lecoufle 1990; D'Amato 1998; ICPS 2022) but the exact species involved are unknown. Polyphagous species like two-spotted spider mites can likely feed on most carnivorous plants.

Other small, red mites that may occur on carnivorous plants are beneficial, so care should be taken to identify mites before control methods are implemented. For example, concrete mites (*Balaustium* spp.) and whirligig mites (*Anystis* spp.) are common predators that are frequently found in open, sunny spots, such as the sides of buildings and on trees and plants. Both groups feed on small, soft-bodied arthropods and eggs so can help suppress pest populations outdoors. They are typically larger (1–2 mm) and more active than spider mites and do not spin webs.

Soil mites is a catchall term for any mite found in soil, but most frequently refers to oribatid mites, which are sometimes called moss mites as they are ubiquitous in moss, leaf litter, and other and other damp areas. They can sometimes colonize indoors plants, especially those grown in high organic media that stays damp. Most oribatid mites are detritivores that feed on decaying plant material and pose no danger to living plants. They may even be beneficial as they can help regulate algae, fungi, and similar organisms growing in the substrate. However, *Scheloribates* mites have a broader feeding biology compared to other oribatids. While an uncommon occurrence, *Scheloribates* have been known to infest and cause direct feeding damage to greenhouse-grown and indoor house plants (R. Norton pers. comm., pers. obs.). The damage is thought to be related to mite feeding on necrotic tissue that then spreads to healthy tissue, but the phenomenon has not been well investigated. *Scheloribates* infestations have not yet been associated with carnivorous plants but



Figures 28–31. Other insects associated with carnivorous plants. (28) Adult and (29) larval fungus gnats can be common in damp areas and are often associated with plant pots. (30) *Sarracenia* pitchers are sometimes colonized by nesting *Isodontia* wasps, which (31) pack their nests with paralyzed katydids. Nesting rates are generally low so should not affect the overall health of the plant. Figure 28 by Whitney Cranshaw, Colorado State University, via Bugwood.org, used under a CC BY 3.0 US Deed license. Figure 29 by Fero Bednar and figures 30 and 31 by Janet Wright, via iNaturalist, used under CC BY-NC 4.0 Deed licenses.

given their broad feeding biology it is likely that they colonize and feed on them. So, in most cases, oribatid infestations are only a nuisance because of their presence but in rare cases infestations can cause direct damage to plants.

Dark-winged fungus gnats are small (1–11 mm, most <5 mm), dark colored flies (Fig. 28). The larvae feed on fungi in moist areas, so they are common in forests, swamps, lawns with thick thatch, decaying vegetation, damp leaf litter, and other outdoor areas that support fungal growth (Fig. 29). In homes, dark-winged fungus gnats are usually associated with plant pots with consistently damp substrate that allows fungi to grow. In most cases, dark-winged fungus gnats are only a nuisance because of their presence. However, populations can build up such that larvae can damage otherwise healthy seedlings by feeding on root hairs and, in extreme circumstances, boring into plant stems (Frank *et al.* 2020b). Adults and larvae can also vector plant fungal pathogens (Harris *et al.* 1996). While no studies have specifically examined the impact of dark-winged fungus gnat infestation on carnivorous plants, they likely follow a similar pattern where low populations are merely a nuisance but high populations may damage plants, especially seedlings, through direct feeding and possibly pathogen transmission.

Grass-carrying wasps (*Isodontia* spp.) are medium sized (16–20 mm) wasps that are usually dark in color but may have a red abdomen or legs and/or thick golden hairs. Sixty-two species occur worldwide (Pulawski 2003). Female wasps build nests by packing strands of grass into pre-existing holes and tight spaces, such as hollow stems, beetle and carpenter bee holes in wood and dead trees, window tracks, folded patio umbrellas, and similar areas (Fig. 30). These grass nests are then provisioned with paralyzed crickets, katydids, and other orthopterans for the young wasps to eat (Fig. 31). *Isodontia apicalis* (=*Chlorion harrisi*), *I. mexicana*, and *I. philadelphica* have been

Table 4. Insecticide recommended for pest control on carnivorous plants in literature and online.

Insecticide type	Insecticide active ingredient	Insecticide class	Reference(s)
Systemic	Acephate	Organophosphate	D'Amato 1998; California Carnivores 2022b; ICPS 2022a
	Acetamiprid	Neonicotinoid	Hewitt-Cooper 2016
	Imidacloprid	Neonicotinoid	Sarracenia Northwest 2010; California Carnivores 2022b; Brandwood 2020; ICPS 2022a; CPN 2023
	Thiacloprid	Neonicotinoid	Hewitt-Cooper 2016
Contact	"Sevin"	Various*	D'Amato 1998; ICPS 2022a, 2023
	Abamectin	Avermectin	ICPS 2022a
	Bacillus thuringiensis (Bt)	Biological	Sarracenia Northwest 2019; ICPS 2022a, b; California Carnivores 2023
	Bifenazate	Bifenazate	ICPS 2022a
	Bifenthrin	Pyrethroid	California Carnivores 2022b; ICPS 2022a
	Cyfluthrin	Pyrethroid	CPN 2023
	Diazanon	Organophosphate	D'Amato 1998
	Horticultural oil	Oils	Succulent Flytraps 2019
	Insecticidal soap	-	Hewitt-Cooper 2016
	Isopropyl alcohol	-	California Carnivores 2022b, 2023; ICPS 2022a
	Malathion	Diazanon	D'Amato 1998
	Neem	Botanical	Sarracenia Northwest 2010
	Permethrin	Pyrethroid	Sarracenia Northwest 2010
	Pyrethrin	Pyrethrin	Sarracenia Northwest 2010; California Carnivores 2022a, b, 2023; ICPS 2022a
	Spinosad	Spinosyns	ICPS 2022a, 2023

*Sevin products have historically used carbaryl as the active ingredient. However, in recent years some products have been changed to bifenthrin, zeta-cypermethrin, and other active ingredients

recorded to nest in *Sarracenia alata*, *S. flava*, *S. jonesii*, *S. leucophylla*, and *S. minor* in eastern North America (Hubbard 1896; Jones 1904; Rau 1935; Fish 1976; Rymal & Folkerts 1982; Rodenas 2012; Rice 2007; Harvard Forest 2021). Colonization of *Sarracenia* by grass-carrying wasps is low, up to 2.5% of pitchers and often less (Jones 1904; Fisher 1976; Rymal & Folkerts 1982), so while the nests stop individual pitchers from capturing prey, the wasps are not a threat to the overall health of a plant. Grass-carrying wasps are not defensive and generally fly away unless grabbed or handled, so growers can leave nests without worry of stings or remove them if they want to allow a pitcher to continue to capture prey.

Published pesticide review.

Only four systemic pesticides were recommended for use in books and other media (Table 4), all of which act as contact pesticides as well. The systemic pesticides were all broad-spectrum products that can control a wide variety of pests. Most (3 of 4) were neonicotinoids. More than half of the 15 contact pesticides recommended in books and other media were biorational products that targeted specific groups of pests (e.g., Bt) or had low residual activity (e.g., soaps and oils). The modes of action were varied.

Most popular books suggested using broad spectrum products that could be used against all or most arthropod pests. They sometimes lack specifics or were vague, such as recommending to "control [thrips] with an insecticide" (Hewitt-Cooper 2016). Recommendations in other media such as nursery websites and YouTube videos were more specific and often recommend specific pesticides for specific pests or carnivorous plant groups.

Survey results.

Seventy-eight survey responses from 52 respondents were received from 1–14 February 2023, of which 47 responses from 25 finished surveys could be analyzed. Of the 25 respondents that completed the survey, 21 were from the United States, two were from the United Kingdom, and one each were from the Philippines and Singapore. Most respondents grew more than 100 individual plants (Table 5). Most pests were reported from plants grown in indoor settings, with a variety of carnivorous plant taxa and pests reported (Tables 6 and 7). Spider mites were the pest reported most frequently (10 reports), followed by aphids (9), scale insects (7), mealybugs (5), thrips (5), soil mites (4), and dark-winged fungus gnats (2).

Table 5. The number of carnivorous plants grown by the survey respondents.

Number of plants grown	Number of respondents
1–9	0
11–50	7
51–100	5
>100	13
Total	25

Respondents reported the use of 14 products used to control pests: one was not a pesticide, five were biorational pesticides, and eight were broad spectrum pesticides (Table 8). The most commonly reported active ingredient, either alone or in combination with other active ingredients, was imidacloprid with 18 responses (40.9% of the total). All other products were reported six or fewer times (13.6% of total or less).

Only two of 25 respondents reported adverse effects of pesticides to plants. One reported that Compo Triple Action was harmful to *Dionaea muscipula*, *Drosera capensis*, and *Pinguicula lusitanica* and one that BioAdvanced 3-in-1 was harmful to an unnamed *Drosera* species.

Table 6. Reported arthropod pests of carnivorous plants grown indoors.				
	Cephalotus	***Dionaea***	***Drosera***	***Heliamphora***
Aphids		2	1	1
Dark-winged fungus gnats				
Mealybugs	1		1	1
Scale insects	1			2
Soil mites	2			
Spider mites	2	2		3
Thrips				
Total	6	4	2	7
	Nepenthes	***Pinguicula***	***Sarracenia***	**Total**
Aphids		1		5
Dark-winged fungus gnats		1		1
Mealybugs			1	4
Scale insects			2	5
Soil mites		2		4
Spider mites	3			10
Thrips	4			4
Total	7	4	3	33

Table 7. Reported arthropod pests of carnivorous plants grown outdoors.				
	Darlingtonia	***Dionaea***	***Drosera***	***Nepenthes***
Aphids	1	2	1	
Scale insects				1
Total	1	2	1	1
	Pinguicula	***Sarracenia***	**Total**	
Aphids			4	
Dark-winged fungus gnats	1		1	
Mealybugs		1	1	
Scale insects		1	2	
Thrips		1	1	
Total	1	3	9	

Table 8. Pesticides and associated that reported by survey respondents.

Product	**Active ingredients**	**Plants used on**	**Number of responses**	**Number of responses that product harmed the plant?**
Rubbing Alcohol	91% isopropyl alcohol	*Drosera*	1	
Avid	Abamectin	*Nepenthes*	1	
Orthene	Acephate	*Sarracenia*	2	
Azamax	Azadirachtin	*Cephalotus*, *Heliamphora*	2	
Bti	Bacillus thuringiensis israelensis	*Pinguicula*	2	
Compo triple action	Deltamethrin, Tebuconazole, Abamectin	*Dionaea*, *Drosera*, *Pinguicula*	4	4
	Dimethoate 4EC	*Nepenthes*	6	
Bayer Rose & Flower	Imidacloprid	*Cephalotus*, *Drosera*	2	
BioAdvanced Fruit, Citrus & Vegetable Insect Control	Imidacloprid	*Cephalotus*, *Heliamphora*	5	
BioAdvanced 3-in-1	Imidacloprid, Tau-fluvalinate, Tebuconazole	*Dionaea*, *Drosera*, *Heliamphora*, *Pinguicula*, *Nepenthes*, *Sarracenia*	11	1 (Drosera)
Neem	Neem oil	*Dionaea*, *Nepenthes*, *Sarracenia*	5	
	Pyrethrin	*Nepenthes*	1	
Monterey	Spinosad	*Nepenthes*	1	
Captain Jack's Dead Bug Brew	Spinosad	*Nepenthes*, *Sarracenia*	2	
Bug Clear		*Nepenthes*	1	

Discussion

Arthropod pests. While the arthropod pests that feed on carnivorous plants are well known in general, only a few specifics are known as there has been no effort to systematically document the pests found on cultivated carnivorous plants and very few pests have been identified to species. Because so little is known, growers have an opportunity to contribute to scientific knowledge. The best way to do this in the United States is to submit pests for identification to local entomologists at state departments of agriculture, local Extension services, or arthropod identification and plant disease laboratories associated with state universities (e.g., the Penn State Insect Identification Lab). Other countries will have different institutions, but often have agencies to identify insect pests. If submitting specimens to experts for identification is not possible, then posting high-quality photographs online is helpful as it preserves the interaction and some pests can be identified to species or another useful taxonomic level based on photographs. The best place to post photos is iNaturalist (inaturalist.org) as it is global in reach, covers all life, can be searched taxonomically, which makes screening photographs of plants for pests much easier, and is used by scientists to conduct research – more than 500 scientific publications have been based on iNaturalist data so far (Skvarla & Fisher 2023).

Aphids are the best studied group of pests, but most species are only reported from one or a few hosts from one or a few areas. In North America, three specialist species have been reported from wild plants, but none have been reported from cultivated plants. This lack of clarity can complicate pest control as a number of polyphagous species that are pests in agricultural crops are resistant to pesticides (Georghiou & Lagunes-Tejada 1991; Silva *et al.* 2012), but it's not clear if pesticide resistance species feed on carnivorous plants. Similarly, the presence of a few aphid-vectored plant viruses in carnivorous plants shows that such viruses can infect cultivated carnivorous plants, but it's not clear how widespread the phenomenon is or which aphids are vectoring the viruses.

In areas where native carnivorous plant-feeding arthropods exist, there is an opportunity to test the host range of those species. For example, will sundew plume moths (*Buckleria parvulus*) in eastern North America feed on cultivated non-native sundews such as *Drosera capensis*? Do *Buckleria negotiosus* in South Africa feed on *Drosera* at all? If growers observe these specialist caterpillars on their sundews, it's likely that any observation they make is new and has never been reported before. Similarly, grass-carrying wasps occur worldwide, but have only been reported from *Sarracenia* in the Southeastern United States. Will species outside of the native range of *Sarracenia* utilize pitchers as nesting areas?

Knowing which arthropod species native to an area can help with conservation as well. For example, growers in North Carolina, especially those that live near wild Venus flytrap colonies, should be aware of Venus flytrap cutworm moths and report potential caterpillars to the appropriate entities, such as the North Carolina Natural Heritage Program and U.S. Fish and Wildlife Service, as any observations of these endangered moths could be critically important to saving the species from extinction.

Pesticides. While a country-level review of the legality of various pesticides is beyond the scope of this article, many of the products suggested in books and other media (Table 4) have been banned by various countries and states around the world. For example, all of the systemic products except bifenthrin have been banned in the European Union, acephate is banned in China and India, and various U.S. states have banned imidacloprid and other neonictinoids. Some of the contact pesticides, particularly malathion, have also been banned and are generally unavailable. This can make

it difficult for home growers to decide what product to use if a specifically recommended active ingredient is unavailable where they live.

Another issue is that some published works recommend specific brand products without specifying the active ingredient. This can create issues when the active ingredient is changed but the product label remains largely unchanged. For example, some sources suggested using Sevin, which historically used carbaryl as the active ingredient. However, in recent years Sevin brand products have changed the active ingredient to any of three different chemicals, none of which are carbaryl. This can create problems if newer chemicals have different phytotoxic effects in plants or if they have different efficacy against pests.

Insecticidal soaps are the only group of pesticides that have multiple recommendations not to use them. The active ingredient in insecticidal soaps are potassium salts of fatty acids and it is variously reported that they harm plants because they are alkaline (D'Amato 1998) or that they break down into potassium in the growing medium (Sarracenia Northwest 2010). Otherwise, it appears that many pesticides are safe to use on carnivorous plants. Commercial growers reported that they use a variety of products without issue on many different plant taxa (California Carnivores 2022a, b; ICPS 2022 a, b; CPN 2023; Table 4) and only two of the twenty-five survey respondents reported possible phytotoxicity issues after applying pesticides. Both products that were reported to harm plants were combination products that include two pesticides (deltamethrin and abamectin or imidacloprid and tau-fluvalinate, respectively) and the fungicide tebuconazole. It may be that tebuconazole, the only active ingredient shared between the two products, has phytotoxic effects when applied to certain plants or in certain situations. Rice (2005) reported that Bayer Rose and Flower Insect Killer, which contains imidacloprid and cyfluthrin, had phytotoxic effects (leaf curling and browning) in some *Dionaea* but not other genera including *Byblis*, *Drosera*, *Genlisea*, *Pinguicula*, or *Sarracenia*, so different effects within and between plant groups is not unknown.

Imidacloprid was recommended by multiple published sources and was the most popular active ingredient amongst respondents, likely owing to its ease of use, broad range of pests killed, wide over-the-counter availability in the United States and high proportion of respondents from that country. Previous reports have indicated that it can be phytotoxic to *Dionaea* (Rice 2005) and one of the products reported to harm plants by survey respondents contained imidacloprid.

In conclusion, while many pesticides are apparently safe for carnivorous plants, some of them (i.e., at least imidacloprid and tebuconazole) should be evaluated for phytotoxicity issues as they may be toxic to some plants in some situations. Additionally, alternatives to imidacloprid should also be assessed due to the unavailability of the chemical in many countries and potential for it to be banned in the United States, either by the federal government or piecemeal by various state governments.

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Comparative shoot morphology between cultivated *Utricularia bremii* plants and those growing in natural habitats in the Czech Republic

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Abstract: In summer 2023, the morphometry of large adult plants of *Utricularia bremii* was studied in an outdoor culture and at three shallow pools in two oligotrophic sand-pits in South Bohemia, Czech Republic, with a focus on shoot length and biomass, shoot branching traits and ecological conditions. Overall, the mean length of main shoots was 34-43 cm (range 23-73 cm) and the shoots bore on average 11-18 branches of three orders. On main shoots, branches were initiated on average every 7.7-9.2 internodes, which indicates a very fast propagation and growth. A new branch is theoretically initiated every ca. 3.3-3.8 days. This study confirms that shallow, well-lit, oligo-mesotrophic, soft-water sand-pit pools may represent an ecological optimum for this species.

Introduction

Utricularia bremii Heer *ex* Kölliker is a temperate perennial aquatic carnivorous plant with a distribution in Central, Western, Northern and North-Eastern Europe (Casper 1974; Taylor 1989; Fleischmann & Schlauer 2014; Adamec 2020). It has usually monomorphic (non-differentiated) shoots up to 50-60 cm long (but commonly only 20-30 cm) that bear both filamentous or flattened photosynthetic "leaves" in regular leaf nodes and 1-2.8 mm long traps (Fig. 1). Rarely, the shoots are partly differentiated into green photosynthetic ones with a lesser number of traps, and paler carnivorous ones with many traps and leaf filaments immersing into a soft substrate (Taylor 1989; Fleischmann & Schlauer 2014; Adamec 2020). Nevertheless, quite similarly as in a 'twin' species, *U. minor* (Adamec & Kučerová 2022), the size and morphology of the shoots are enormously variable: a very slender thread-like habit occurring on emergent, wet sandy barren soils may be changed to more robust, frequently branched habit when growing submerged in more trophic waters. Therefore, the habit of *U. bremii* markedly depends on ecological conditions (mainly water depth or terrestrial growth or trophic level) and the species can be considered fully amphibious. During June to August, the plants form an erect raceme inflorescence 5-50 cm long emerging from the water and bearing 2-14 light-yellow flowers (Taylor 1989; Fleischmann & Schlauer 2014; Adamec 2020). However, inflorescences only ca. 10-25 cm high were observed repeatedly at several Czech sites where the plants prolifically flower (L. Adamec, pers. observ.). In spite of spectacular yellow flowers (Fig. 2), the plants are usually sterile due to pollen malformation and do not set seeds (Casper & Manitz 1975; Taylor 1989; Beretta *et al.* 2014). The shape of corolla is basically the only determination mark between *U. bremii* and *U. minor* (Fleischmann & Schlauer 2014; Adamec 2020). As observed at South Bohemian sites in the Czech Republic repeatedly, flowering of *U. bremii* requires

longer periods of warm summer weather, shallow water (1-5 cm) with stable level (L. Adamec, pers. observ.) – the same requirements which allow flowering of similarly rare European *Utricularia* species (see Adamec 2020).

Utricularia bremii grows with a highly scattered distribution in peatbogs, fens, peaty fishponds, peaty meadows, backwater pools, springs, and also in small shallow sand-pits. It usually grows in very shallow water 2-20 cm deep and often semi-terrestrially. The plants growing in very shallow water are usually loosely anchored in the substrate, while those growing in deeper water (>25 cm) are mostly floating freely at the surface. As opposed to the very similar and much more common and eurytopic *U. minor, U. bremii* as a partly stenotopic species grows within the narrow pH from ca. 5.0 mesotrophic waters (for the review, see Adamec 2020), while *U. minor* within the wide pH from 3.9 to 7.5 in very soft to slightly hard waters and in clear to strongly dystrophic (humic), brownish, oligo-to 9.2. At the reported *U. bremii* sites, electrical conductivity ranged from 1.2-42.4 mS/m, total alkalinity from 0.11-0.46 meq/L, free CO_2 concentration from 0.11-0.34 mM, NH_4^+-N from 0.2-41 µg/L, PO_4-P from 1.9-25 µg/L and NO_3^--N was 0.0 µg/L. However, as the reported sites were mainly soft-water sand-pits, it is possible to consider that the ecological amplitude of *U. bremii* is much wider. *Utricularia bremii* usually grows together with *U. australis* (Adamec 2020). In the Czech Republic, it is declared a critically endangered species (C1) of the Czech flora (Grulich 2017) with ca. 10 natural sites mostly in W, S and N Bohemia (Adamec 2020) and is a legally protected species. Between 2008-2012, local *U. bremii* has been introduced to five oligotrophic shallow sand-pits in the Třeboň basin, S Bohemia, Czech Republic, where large populations have arisen since (Adamec 2020). As judged to several Czech sites, both species-poor, very shallow (0.5-5 cm) microhabitats in

Figure 1: Detailed view on a robust, markedly branched plant of *U. bremii* collected from the Suchdol Southern pool. Note partly decaying basal leaf nodes stained by ferric precipitates. The white bar indicates 1 cm.

well-lit shallow sand-pit pools without water level fluctuations and shaded dystrophic forest pools may represent an ecological optimum for this species, which is characterized by high cover and stand biomass and prolific flowering (Adamec 2020).

As opposed to *U. australis* and *U. vulgaris*, which maintain more or less constant shoot length at maturity during a great deal of the growing season ('conveyer-belt' system of shoot growth; Adamec 2018), *U. bremii* (and also *U. minor*) rather increase gradually their mother shoot length up to the initial stage of autumnal turion formation (Adamec 2020). Afterwards, the mother shoots are gradually shortened up to the turion length due to the decay of senescent basal shoot segments. Owing to the rarity of *U. bremii*, very few detailed data on its morphometry, growth traits, and eco-physiology are known (see Taylor 1989; Fleischmann & Schlauer 2014; Adamec 2018, 2020). The rapid vegetative growth of *U. bremii* includes both rapid apical shoot growth of mother shoots and high branching rate (Adamec 2011, 2018, 2020). The mean apical shoot growth rate of 2.40±0.14 leaf nodes day^{-1} was found in a greenhouse-growth experiment in *U. bremii* shoot segments fed on prey, while non-fed control plants formed only 1.30±0.15 nodes day^{-1} and 3.3 times less branched (Adamec 2011). Moreover, fed plants branched after each ca. 12 leaf nodes on the main shoot ('branching rate') and/or each 5.0 days ('branching frequency'). Feeding on prey in *U. bremii* is thus just as important for supporting the growth as in other aquatic carnivorous plants (cf. Adamec 2018, 2020).

Here, I present morphometric investigations of robust *U. bremii* shoots in its dense stands at three microsites at two artificial sites in shallow oligo-mesotrophic, former sand-pits in the Czech Republic, and in an outdoor culture in the Institute of Botany at Třeboň, Czech Republic. An

Figure 2: Detail of a typically flat and wide corolla of *U. bremii* from the Suchdol sand-pit.

emphasis is put on shoot length and biomass, shoot branching traits, and ecological conditions. This study tightly follows up on a recent paper by Adamec & Kučerová (2022) conducted on *U. minor* in the same region and allows to better compare both species.

Site description

Plants of *U. bremii* were investigated in an 80 cm deep, 2 m^2 outdoor plastic container in the collection of aquatic and wetland plants in the Institute of Botany, Czech Academy of Sciences, at Třeboň, Czech Republic, in two small shallow pools (denoted as Southern and Northern) in a former sand-pit near Suchdol nad Lužnicí, and in a shallow pool in an old sand-pit near Cep. All these sites lie in the Třeboňsko Biosphere Reserve and Protected Landscape Area in S Bohemia, Czech Republic (ca. 49°N, 15°E, elevation 430-445 m a.s.l.).

The outdoor container in the collection was kept as a 'moderately dystrophic pool' with slightly brownish water and a variety of submerged and emergent plants. The container was shaded by a green plastic gardener's net and the PAR irradiance at the surface was reduced to ca. 30-40% of that in the open. A dense stand of *U. bremii* was distributed from the surface up to the depth of ca. 25 cm. Plant dominants in the container were *Carex limosa*, *Eriophorum angustifolium*, *Comarum palustre*, and *Nymphaea candida.* Medium-hard tap water was used to cover water losses.

In the Cep sand-pit, rather slender *U. bremii* plants were collected in a large shallow pool (ca. 0.1 ha) from a dense stand around 2 m from the shore at a water depth of 20-25 cm (Fig. 3).

Figure 3: Shallow shore of the Cep sand-pit with dominant but slender *U. bremii.*

Juncus bulbosus, *J. effusus*, *Eleocharis acicularis*, *Glyceria fluitans*, *Utricularia australis*, *Peplis portula*, and a submerged acidophilous *Sphagnum cuspidatum* were the local dominant plants growing in full sunlight. A clayish-organic light sediment 2-3 cm deep occurred on the bottom.

In the Suchdol sand-pit, *U. bremii* plants were collected from two small adjacent pools ca. 15 m^2 large which were only 3 m away from each other, i.e., the Southern and Northern pool. The Southern pool (Fig. 4) was 10-25 cm deep (the water level in both pools was lower by 6 cm at the time of sampling than the normal one is) and *U. bremii* plants here were more robust than in the Northern pool. The Northern pool (Fig. 5) was 10-20 cm deep. A clayish-organic sediment ca. 10 cm deep lay on the bottom in both pools. It was covered by loose, brown-red ferric precipitates of $Fe(OH)_3$ to which *U. bremii* shoots were immersed (Fig. 6). Plant dominants in both pools were *U. australis*, *Alisma plantago-aquatica*, *Typha latifolia*, and *Juncus effusus* on the shores. Pools in both sand-pits were supplied mainly with rain water and, therefore, they contained very soft water.

Methods

The sampling of *U. bremii* plants from all four microsites was conducted between 29 July and 2 August 2023 when long shoots reached around their maximal lengths and started decaying at their bases (Fig. 1) where senescent turion leaves were usually present. At each of the four microsites, 14 large intact plants were very carefully separated from neighboring plants, deprived of sessile organisms and washed gently in the pool water. An emphasis was put to that each sampled plant was as long, branched and intact as possible. The very fine shoots were

Figure 4: The shallow Southern pool in the Suchdol sand-pit with robust *U. bremii*.

Figure 5: The very shallow and densely overgrown Northern pool in the Suchdol sand-pit.

rather entangled with each other and it was very difficult to separate quite intact plant individuals. Several plants were slightly damaged and, thus, the estimated values have to be considered slightly conservatively. The collected plants did not flower. Each wet plant was put into a plastic bag without water and carefully transported to the laboratory for processing. At each microsite, electrical conductivity was measured using a pocket conductometer and water samples were collected for estimation of pH and total alkalinity in the laboratory as well as for mineral nutrient analyses. Free CO_2 concentration was calculated from pH and total alkalinity (for all analyses, see Adamec 2009).

The detailed shoot structure was estimated in all plants (Adamec & Kučerová 2022): total main shoot length in terms of cm and the number of mature leaf nodes, number of 1st- and 2nd- plus 3rd-order branches and their lengths in terms of the number of mature leaf nodes, number of internodes between two successive branches in main shoots and branches, and the dry weights (DW, 80°C). Every distinguishable axillary bud >1 mm long was considered a branch as it could give a rise of a new branch. Using a binocular loupe, the length of the largest trap (to the nearest ca. 0.2 mm) and the proportion of traps with caught prey (or brown precipitate containing humic acids or detritus) were estimated in 30 traps in the middle part of the shoots of 3-4 plants. As the individual plants had different numbers of branches, means of each of 14 plants were averaged. Means ±SE intervals and ranges for individual plants are shown. The significant difference in parameters between the microsites was tested using a 1-way ANOVA with a Tukey HSD test for multiple comparisons. The interrelationship of the apical shoot growth rate (ASGR, defined as the number of newly formed leaf nodes per day) of main shoots and branches was also estimated (see Adamec & Kučerová 2022).

Figure 6: Dense stand of *U. bremii* immersed to ferric precipitates in the Suchdol Southern pool.

New branches are initiated on the apex of the main shoot and grow together with the main shoot but their ASGR may be different. When the number of mature leaf nodes from the apex is estimated in main shoots and long branches in *Utricularia* plants then the linear regression of these couples of data determines the ratio between the ASGRs of branches and main shoots. If the ratio is 1, the ASGR of both organs is the same but usually it is <1 indicating that the growth of branches is somewhat inhibited by the main shoot.

Results and discussion

Total alkalinity and electrical conductivity in the culture water were much higher than those at the three microsites in sand-pits where the waters were extremely soft and rather oligotrophic (Table 1). The Suchdol Northern pool with a denser aquatic vegetation (Fig. 5) was less oligotrophic than the Southern pool. Judging to pH values and zero total alkalinity at three microsites in both sand-pits, their free CO_2 concentration could be around two orders of magnitude lower than that in the culture and, thus, very suboptimal (espec. in the Northern pool). In general, all parameters of water chemistry in the waters are within the limits reported in the literature for *U. bremii* (cf. Adamec 2020).

The mean lengths of main shoots of large *U. bremii* plants were not significantly different at four microsites and varied between 34-43 cm (Table 2). The longest plants measured from 42 cm (Cep sand-pit) to 73 cm (Suchdol: Southern pool). However, the mean number of mature nodes of main

Table 1. Water chemistry at microsites in investigated dense *Utricularia bremii* stands. TA, total alkalinity; EC, electrical conductivity.

Microsite	pH	TA	CO_2	EC	NO_3^--N	NH_4^+-N	PO_4-P
		(meq/L)	(mM)	(mS/m)	(µg/L)		
Culture	6.11	0.73	1.32	16.3	13.5	29.2	1.2
Cep sand-pit	5.81	0.00	–	1.70	0.0	4.2	5.8
Suchdol sand-	6.49	0.00	–	1.61	0.0	7.2	8.8
pit: Southern							
Suchdol sand-	6.72	0.00	–	2.22	0.0	13.5	8.6
pit: Northern							

shoots (from 55-82) did not correlate with the shoot length as the shortest main shoots at Cep and Suchdol-Southern contained the most nodes. Over all, the number of main shoot nodes ranged from 40-96. The longest *U. bremii* plant in this study (73 cm) does not extend much the values reported in the literature (50-60 cm, see Adamec 2020). Moreover, the comparison of four micropopulations shows that the length of the main shoot may not be a good criterion of plant size. The long plants had on average 8.4-11.1 1st-order branches but no significant difference was found among the micropopulations though great differences occurred within each micropopulation. Unlike the mean number of 2nd-+3rd-order branches greatly differed among micropopulations and was the lowest at Cep and Suchdol-Northern (2.9-3.0). The mean number of all branches ranged from 11.4 (Suchdol-Northern) to 18.2 (Suchdol-Southern) but very high individual variability occurred within each micropopulation. The maximal length of traps was 1.2 mm at Cep, but 1.5 mm at the other microsites. The proportion of mature traps with caught prey (or a precipitate containing humic acids or detritus) was only up to 30% at Cep, but 40-60% at the other microsites.

Plant DW integrated properly the biomass of both the main shoots and all branches and expressed the size of plants best of all parameters. Marked and significant differences in mean plant DW were found between microsites (Table 2). The highest mean DW was in the plants at Suchdol-Southern (41.0 mg) and in the culture (29.9 mg) followed by Suchdol-Northern (18.2 mg) and Cep (8.8 mg). Similar to other morphometric parameters estimated, the plant DW was very variable within each micropopulation (by the factor of 3-7) and totally ranged from 4.2-103 mg. Although the number of internodes between two successive branches both on the main shoots and branches were extremely variable (total range of 1-39), the means were very similar on the same organ type among the micropopulations as well as between both types of organs for each micropopulation (Table 2). The means for main shoots were from 7.8-9.2. The linear regression of the number of leaf nodes of main shoots and branches confirmed a highly significant correlation ($P<0.001$-0.000001; n=8-23) within each micropopulation. The ratio of ASGRs for branches and main shoots was 0.733 for the culture, 0.947 at Cep, 0.667 at Suchdol Southern and 0.866 at Suchdol Northern. Thus, in all micropopulations, the apical growth rate of 1st-order branches was only 67-95% of that of main shoots. These values may express the strength of apical dominance of the main shoot apex as a sink for both mineral and organic nutrients from mature shoot segments. They are very similar to those found in closely related *U. minor* (0.83) and other aquatic carnivorous plant species (0.65-0.85, see Adamec & Kučerová 2022) and suggest that this relationship between the ASGRs can be generalized for this plant group. However, the significant

Table 2. Morphometric characteristics of robust *Utricularia bremii* plants in culture in the Institute of Botany at Třeboň and in three shallow oligotrophic pools in two sand-pits in S Bohemia, Czech Republic. Numbers of internodes between two branches on the main shoot and branches are shown. DW, dry weight. Means ±SE intervals (italics) based on averages for individual plants are shown, n=14. Range of values shown for individual plants. Different letters within the columns for variants denote statistically significant difference at P<0.05 (1-way ANOVA).

Microsite	**Main shoot length (cm)**	**Main shoot nodes**	**Plant DW (mg)**	**Number of branches per plant**			**Internodes between two branches**	
				1st-order	**2nd-+3rd-order**	**All**	**Main shoots**	**Branches**
Culture	38.3[a]	55.1[a]	29.9[ac]	9.1[a]	6.2[ab]	15.3[ab]	7.8[a]	8.3[a]
	±2.8	*±2.9*	*±3.1*	*±0.8*	*±0.9*	*±1.6*	*±0.5*	*±0.3*
	23.2–64.5	40–75	11.4–51.3	6–15	2–15	8–25	1–17	3–17
Cep sand-pit	34.1[a]	81.7[b]	8.8[b]	11.1[a]	2.9[a]	14.0[ab]	7.8[a]	8.5[a]
	±1.2	*±3.0*	*±0.8*	*±1.2*	*±0.8*	*±1.6*	*±1.0*	*±1.1*
	25.2–41.5	52–96	4.2–13.6	3–19	0–10	3–25	1–39	1–27
Suchdol sand-pit: Southern	42.8[a]	59.4[a]	41.0[a]	9.6[a]	8.6[b]	18.2[a]	8.1[a]	7.8[a]
	±2.9	*±2.7*	*±6.8*	*±0.8*	*±1.6*	*±2.1*	*±0.5*	*±0.3*
	34.1–73.0	45–82	15.6–103	6–16	1–20	7–32	2–25	3–16
Suchdol sand-pit: Northern	37.5[a]	64.4[a]	18.2[bc]	8.4[a]	3.0[a]	11.4[b]	9.2[a]	7.7[a]
	±2.3	*±3.0*	*±1.9*	*±0.6*	*±0.6*	*±1.1*	*±0.3*	*±0.5*
	28.7–62.0	53–94	9.0–31.8	4–12	0–7	6–18	3–16	2–16

differences between four *U. bremii* micropopulations indicate that physiological relationships between main shoots and branches are modulated by environmental conditions such as CO_2 or prey availability.

The most of the selected *U. bremii* plants in this study bore senescent shortened turion leaves at their shoot bases at all microsites. This means that these plants started their seasonal, spring growth from turions, but not from separated branches later in the season. The comparison of morphometric data on robust *U. bremii* (Table 2) and *U. minor* plants (Adamec & Kučerová 2022) confirms that on the level of length and number of nodes of the main shoot, number of 1st-order branches and plant DW, both species are very similar to each other as the mean as well as individual values greatly overlap though *U. bremii* in this study was somewhat more branched. However, an evident difference between both closely related species was found in the branching rate of main shoots and branches: in *U. minor*, the mean values were 12.2 and 16.8 internodes, respectively (Adamec & Kučerová 2022, cf. Table 2). The lower branching rate in *U. minor* could be due to frequent flowering and seed set since in an ecologically similar *Aldrovanda vesiculosa*, developing flowers competed with shoot apices and reduced markedly the branching rate (Cross *et al.* 2016). Moreover, it is well known in several *Utricularia* species and *Aldrovanda* that branching rate depends strongly on CO_2 or prey availability (Adamec 2018). Thus, put together, these plants can regulate not only the number of formed branches, but also their growth rate. At four *U. bremii* microsites, a new branch

was initiated on average after each 7.8-9.2 internodes on the main shoots (Table 2). Considering an ASGR of 2.4 internodes/day in *U. bremii* (Adamec 2011), a new branch is theoretically initiated as early as every ca. 3.3-3.8 days, while it can be every ca. 5.1 days in *U. minor* (Adamec & Kučerová 2022). Thus, *U. bremii* could propagate faster.

Plant DW could be considered the best criterion of size and fitness of *U. bremii*. Out of four micropopulations, the smallest and the most slender shoots were clearly at the Cep sand-pit, which was evidently the most oligotrophic of all microsites (Table 1) and where the plants also caught the minimum of prey. This result may be confirmed by a greenhouse-growth experiment (Adamec 2011) that optimal growth conditions for this species include mainly relatively high CO_2 concentration and prey availability but low cover of aquatic plants, while water hardness is not important. As concluded also in this study, optimal ecological factors for *U. bremii* can be met in shallow (10-25 cm), well-lit pools in oligo-mesotrophic sand-pits which represent one out of optimal habitats for this species (Adamec 2020). Moreover, eutrophic waters are excluded for this species. It should be added that no *U. bremii* plants flowered at the four microsites at the sampling time due to water level fluctuations before. It has been observed in shallow Czech sand-pits repeatedly (Adamec 2020) that *U. bremii* flowers prolifically only in very shallow pools (1-5 cm), while no flowering usually occurs in deeper waters (>12-15 cm).

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N. ventricosa Porcelain, Bungabon spotted, black peristome, pink
N. vogelii

Review: A Greenhorn Naturalist in Borneo

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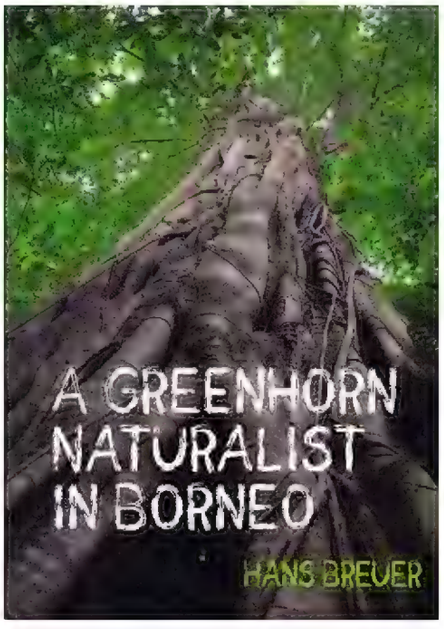

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"He (Dr. Charles Clarke) showed a photo of a gallery forest and asked the audience what they thought they were looking at. The predictable answers ranged from 'trees' to 'forest', but Dr. Clarke dismissed them all. You're wrong," he replied sternly. "You're not looking at a forest. You're looking at hundred million leeches disguised as forest."
(Lecture at the *Nepenthes* Summit in Kuching, Malaysia. 2007)

To say it straight away, Hans Breuer, a German citizen living in Taiwan, is no longer a greenhorn. His first encounter with the magnificent flora and fauna of Borneo inspired the author with his hobby of carnivorous pitcher plants (*Nepenthes*) to such an extent that he moved with his wife and two sons from Taiwan to Sarawak, a Malaysian state on the tropical island. Over the next nine years, he never missed an opportunity to explore its unique ancient rainforests. This resulted in an increasingly profound knowledge of reptiles and snakes in particular. However, the book is expressly not limited to the search for *Nepenthes* and snakes, but goes far beyond that. Up close and not always without consequences, Hans Breuer encounters a number of the planet's most fascinating creatures. Here is an excerpt:

> With its giant eyes, round bear ears and tiny cat nose, the loris was an overdose of adorability. The white lines around its eyes endowed it with an air of profound sorrow, and everything about it just screamed, "Please hug and love me!". "This is a slow loris, a close relative of apes and monkeys," I explained.
>
> "… the bad part is, that it's a dangerous animal. Lorises are the only venomous primates in the world, and this one could dish out serious harm. So we will stay the hell away from him" – "Also, loris bites are among the most powerful in the world."
>
> "Seriously, Dad? A poisonous monkey? How dumb exactly do you think we are?"
>
> The boys stared at the loris with open mouths. A venomous teddy bear with hyena jaws? Coooooool!

Encounters with locals who make money by trading wild animals and plants may also be delicate. Although officially prohibited, this is part of everyday life on the edge of the jungle – often under the watchful eyes of the police. With a critical view of what is happening, the author describes in his empathetic way, without exaggerated rhetoric, how dramatic the situation really is for the biodiversity in Borneo's last primeval forests.

Apart from that, reading the book remains enjoyable, as the subtle humor always comes across with well-placed pointed remarks that make you smile, often spiced up with a likeable dose of self-irony. Hans Breuer works as a freelance translator. He studied sinology at the University of Bochum and speaks fluent Chinese besides German and English. The resulting linguistic fluency always sparks a magnificent mental cinema that creates the illusion of being there. Even the book's publisher, which usually publishes in "British English", acknowledges this. As a special exception, he accepts Hans Breuer's "General American" unchanged with the justification (Publisher's Note):

> As Hans Breuer's English is of the international/US variety and his writing is so wonderful idiosyncratic (as you're about to find out), we've broken the mould of our UK English style in order to retain nearly all of his preferred spellings, vocabulary, punctuation and syntax. Vive la difference!

Even those who prefer a more scientific approach will be served. Not only by the included scientific names according to Linné's binary nomenclature, with genus and species. The foreword was written by the well-known naturalist, author, and photographer Chien Lee from Kuching, a volunteer at the Universiti Malaysia Sarawak. With his profound knowledge of the flora and fauna of Borneo and his masterful ability to spot perfectly camouflaged animals even in the twilight, Chien Lee accompanies the "greenhorn" Hans Breuer on many excursions. Of course, the famous *Nepenthes* of Borneo also come in front of the camera. They inspired the first European explorers just as much as they do modern scientists today. Hans Breuer mentions how researchers discovered that bats live in the pitchers of *Nepenthes hemsleyana*. Particularly exciting: the pitcher-shaped insect traps of this species, which climbs high into the trees, have been optimized by adaptation so that

Hans Breuer in Borneo.

they reflect the ultrasonic calls of approaching bats to enable them to find their pitcher dwellings easily. In return, the droppings of the "tenants" serve as optimal fertilizer.

The nocturnal photo safaris for snakes in an abundance of nature full of amphibians, bizarre insects and constantly new and surprising encounters make for exciting reading. Just like the story about the rediscovery of the "rarest lizard in the world" (*Lanthanotus borneensis*), currently the only surviving relative of a fossil from the Cretaceous period, which is considered an ancestor of snakes. As Hans Breuer himself notes, "*I had the great fortune to experience it from a front row seat.*" In order to maintain the suspense, I don't want to give too much away. But what happens is an example of how dangerous the internet has meanwhile become for the survival of rare species. Triggered by serious publications of newly discovered species in scientific media, it sometimes takes only weeks, if not just days, for the first targeted inquiries and orders from unscrupulous "must-always-have-the-hottest-stuff" freaks to arrive directly at the edge of the jungle via social media from all over the world. With this story, the author shows how the inconceivable destruction of biodiversity, even in protected areas, is becoming a perverse and almost commonplace online business.

I read *A Greenhorn Naturalist in Borneo* with great pleasure and can recommend the book wholeheartedly. By no means only to carnivorous plant enthusiasts, who are entertainingly picked up on the very first pages when the author discovers his love for the pitcher plants, which many of us can relate to from our own experience. What follows is a humorous, adventurous, and profound declaration of love to the wonderful nature of the last primeval forests with their biodiversity. It is therefore not easy to answer the question of what I liked less about this book. Perhaps there could have been even a few more than "only" 160+ photos. Also, in the picture of a sundew labeled as *Drosera spatulata* var. *bakoensis*, I rather recognize a *Drosera burmannii*, but this is almost irrelevant in view of the many positive aspects of the book.

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New cultivars

Keywords: cultivar, *Sarracenia purpurea* subsp. *venosa* 'Cilum', *Sarracenia* 'Brooks Garcia'.
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Abstract: Two new carnivorous plant cultivars are named and described: *Sarracenia purpurea* subsp. *venosa* 'Cilum', *Sarracenia* 'Brooks Garcia'.

Sarracenia purpurea subsp. *venosa* 'Cilum'

Submitted: 22 January 2024

In the winter of 2020, through exchanges with other carnivorous plant grower friends, I came into possession of some seedlings of *Sarracenia purpurea* subsp. *venosa* × self from a sowing in winter 2019. Some of these seedlings were in turn exchanged, and I kept for myself two of those that had characteristics that struck me the most. By necessity, I gave one of these two plants to a friend of mine, who at the end of 2022 called to tell me to come and get it because the pigeons had destroyed it. I planted it in a new pot and in spring 2023, it started to produce huge, low and squat traps like many of the clones of *Sarracenia purpurea* subsp. *venous* presently in circulation, but with an exaggerated size, almost the size of a fist. *Sarracenia purpurea* subsp. *venosa* 'Cilum' (Fig. 1) is a very vigorous and fast-growing clone, in the spring period it has a lighter color of the leaves, which at the end of summer vary from dark red to purple. The color of the flower is red.

To keep the cultivar's characteristics, *Sarracenia purpurea* subsp. *venosa* 'Cilum' must be propagated by vegetative means only

—Giuseppe Grossi • Montescaglioso (MT) • Italy • pinguicularumcp@gmail.com

Figure 1: *Sarracenia purpurea* subsp. *venosa* 'Cilum'

Submitted: 29 January 2024

Formerly known as "It's Complicated," *Sarracenia* 'Brooks Garcia' is a very complex hybrid of (*Sarracenia* 'Leah Wilkerson' × *S. alata*) × (*S. psittacina* × (*S. purpurea* × *S. minor*)) created by Brooks himself some years ago. He had several siblings from this cross and gifted one to me in March of 2020. To be honest, I didn't think much of it that first season as it was small and only put up one pitcher in the fall. As the next two seasons progressed, I started noticing this plant more and more in my collection and soon realized it was turning into something special.

Sarracenia 'Brooks Garcia' is a stunning and prolific pitcher plant forming tight clumps in cultivation. It produces beautiful dark purple, chunky pitchers averaging 65 cm or more on older/mature plants. Pitchers start out light red (Fig. 2A) but quickly darken to a deep, deep purple (Fig. 2B) as they age in the sun. They also have a downward angular nectar roll giving the peristome an "open mouth" appearance. It produces a spring and fall flush of sturdy upright pitchers with the fall flush being the most prominent. The flowers are also unique as they are completely red with a single creamy, white vertical stripe extending the majority of the length of all five petals (Fig. 2C).

I coined the name 'Brooks Garcia' in honor of the man who created this beauty but also who made it possible for so many growers to enjoy so many wonderful *Sarracenia* discovered and created by the man himself over the past several decades.

This plant should be reproduced only by divisions/cuttings to ensure its unique characteristics are maintained.

—Fred Passkiewicz • North Carolina • USA • pasky@twc.com

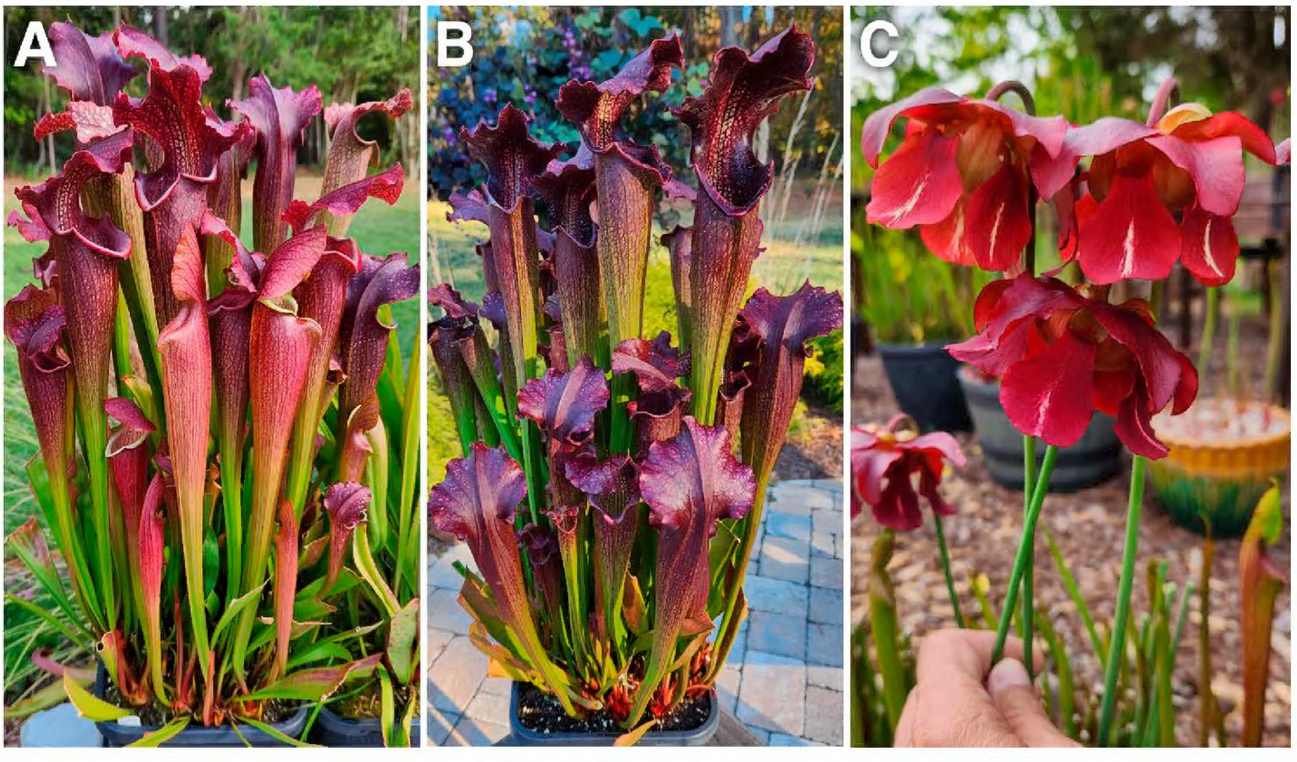

Figure 2: *Sarracenia* 'Brooks Garcia' pitchers in (A) spring, (B) summer, and (C) flowers.